# Systematic Zoology

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| | | |
|---|---|---|
| **Natural Hybridization in Fishes** | ***C. L. Hubbs*** | **1** |
| **Variation and Hybridization in Shrews** | ***R. L. Rudd*** | **21** |
| **Sympatry, Allopatry, and Subspecies in Birds** | ***K. C. Parkes*** | **35** |
| **An Invitation to Systematic Zoologists** | ***O. E. Sette*** | **40** |
| **Gregg: "The Language of Taxonomy"** | ***R. E. Blackwelder*** | **41** |
| **Are Coelenterates Degenerate?** | ***M. W. de Laubenfels*** | **43** |
| **Random Fixation in Fleas** | ***R. Stark*** | **45** |


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# Systematic Zoology

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# Hybridization between Fish Species in Nature

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CARL L. HUBBS

THE Jordan school of ichthyology, in which I was nurtured, held steadfastly to the view that the lines between fish species are almost never crossed. This mistaken idea was perhaps in part a holdover of the pre-Darwinian concept of the immutability of species, but was, more pointedly, a reaction against the tendency of some European ichthyologists to explain as hybrids specimens that proved difficult to identify. This view that there is little or no natural hybridization between fish species may be further attributed to the circumstance that systematic ichthyology in America from about 1890 to 1920 was still essentially in the exploratory and species-naming stage, and dealt chiefly with marine fishes, which, as I shall point out, hybridize much less often than do freshwater fishes.

Early in my ichthyological career I encountered evidence that fish species do cross in nature, at times in considerable frequency. The analysis of such hybridization has ever since engaged my attention, in so far as other activities would allow. This report lays particular emphasis on the researches that I have conducted during the past thirty-five years, largely with the collaboration of my wife and of several students and colleagues, to all of whom I pay tribute. They might all appear as co-authors of this report. The studies continue.

During the first ten years of my intensive studies of the freshwater fishes of North America, from 1919 to 1929, I gathered strong circumstantial indications that the species lines are rather often crossed in nature, and during the following fifteen years, from 1929 to 1944, I was able, with the constant aid of Mrs. Hubbs, to confirm these indications, not only by the accumulation of much more circumstantial evidence, in part subjected to critical statistical analysis, but also by breeding experiments in the aquarium of the Division of Fishes of the then new Museum of Zoology at the University of Michigan.

### *Sunfish Hybrids*

The first main project in this aquarium was the experimental verification of extensive hybridization between the well-known species of sunfish. I had already concluded, on the basis of circumstantial evidence, that certain supposed species had been based on interspecific crosses. The commonest of these, known as *Lepomis euryorus*, I had treated as a natural hybrid between the green sunfish and the pumpkinseed. By placing a male of the one species with a female of the other we soon were elated to observe the characteristic nuptial gyration of sunfishes, followed by the laying of eggs, some of which hatched. And from the eggs that hatched we developed a considerable number of the miscegenates into large adults. The characters matched those of the supposed species *euryorus* and were intermediate between those of the parental species. Similarly, we produced fine adults of the hybrid between the green sunfish and the bluegill. This hybrid cross, also with intermediate characters, had been passing under the name of *Lepomis ischyrus*. Other combinations were effected. Most of the interbreeding was quite voluntary; some was induced by pituitary injections.

From our studies of sunfish hybrids we learned many of the basic facts regarding the interspecific hybridization of these

fishes. As already mentioned, the hybrids are intermediate in taxonomic characters between the parental species. They differ from either parental type, however, in several respects, all attributable to the still poorly understood phenomenon of heterosis, or hybrid vigor. That they grow faster than either parental species was shown by the analyses of size frequencies at determined ages in nature and by measurements of growth in aquarium and pond. The hybrids dominate in the social hierarchy (known in fishes as the nip order). When a mixed group is fed, the hybrids, larger and more vigorous than the pure species, take the food first. In general activity, as in holding fins erect (an indication of vigor), and in the depth, brightness, and intensity of color, the hybrids excel. The great majority of the hybrids in nature as well as in captivity are males. The hybrid males construct, fan, and guard their gravel nests with unusual vigor over a prolonged period, but to no avail, for they are sterile. Sections of the testes of hybrids, whether bred in tanks or caught in nature, show marked abnormalities. In the hybrids the tubules of the testis are often vacuolated and the spermatozoa, when produced, vary greatly in size. When stripped from the hybrids some of the spermatozoa are relatively so immense that the beating of the tails merely rolls them along. The abnormal spermatogenesis of the natural hybrids confirms their identification as hybrids and helps to explain their infertility.

The frequency of hybridization in nature between sunfish species seems to be determined by several ecological factors. There is a relatively high incidence of hybridization in ponds largely filled with vegetation and with very limited gravel areas, where the spawning fish are unduly crowded. Great scarcity of one species coupled with the abundance of another often leads to hybridization: the individuals of the sparse species seem to have difficulty in finding their proper mates. The introduction of a species into a pond inhabited only by other species is also conducive to interbreeding. This is true even for species that elsewhere have come to live together with little or no crossing. In some ponds the observed incidence of hybridization rises to over 10 percent.

In one stream near Ann Arbor I found about 95 percent of the sunfish to be hybrids between the green sunfish and the pumpkinseed. This finding, made early in the study, baffled me at first. On a visit to the Northville Hatchery near Ann Arbor the superintendent complained that the sunfish he had taken in the stream to serve as breeders had not bred in the pond. He scooped out a net full of what I at once recognized as hybrids. How could sterile hybrids, almost all males, attain a 95 percent dominance? I wracked my brain for an answer, which finally took form. There must be, I hypothesized, a pond downstream inhabited by the parental species, which cross occasionally, and the hybrids because of their superior vigor counter the stream current to reach the vicinity of the hatchery. I called the superintendent and learned that there was indeed a pond five miles downstream. We then seined in the pond just what the "desperation hypothesis" called for—the parental species and a few hybrids!

Ordinarily the sunfish hybrids are definitely intermediate and do not grade into either parental type. In three places, however, it was found that the characters of the especially abundant hybrids graded into those of each parental species. At each place the hybrids were further exceptional in that they were not predominantly males. At these three isolated spots, the genes were probably being exchanged—a point of considerable speciational significance.

### *The Case of the "Amazon Molly"*

While we were still engaged in the experimental confirmation of interspecific hybridization in the sunfishes, fishes collected in northeastern Mexico by Drs.

Myron Gordon and Edwin P. Creaser posed a problem that cried for experimental attack. *Mollienisia formosa*, a species of the viviparous topminnow family Poeciliidae, was brought back in only one sex: all of the many specimens were female. Since this nominal species is intermediate between the sailfin molly (*Mollienisia latipinna*) and *Mollienisia sphenops*, hybridization was suspected. We secured live material of all three types and in 1932 inaugurated a twelve-year program of intensive breeding experiments with these three species, and many others.

We proceeded at once to test the reproductive behavior of the species of which only females had been collected. We promptly mated some of these females, which we termed "Amazon mollies," with the two suspected parental types. One of these, *Mollienisia latipinna*, has a longer dorsal fin than *formosa*, originating farther forward and with more rays (13 to 15 instead of 10 to 12); and it has a deeper and more strongly striped body. *Mollienisia sphenops*, the other suspected parental form, has in contrast a shorter dorsal fin than *formosa*, originating farther back and with fewer rays (usually 9 in the subspecies used), and it has a slenderer body with the streaks poorly developed. We soon obtained broods of young, all of which, in confirmation of the seemingly impossible hypothesis that I was forced to erect, proved to be females exactly like their mothers, without any trace of the distinctive paternal characters! Crossing *latipinna* and *sphenops* reciprocally, we obtained hybrids almost exactly like the all-female *formosa*, yet these laboratory-bred hybrids were bisexual, and produced intermediate offspring on backcrosses. In our preliminary note in *Science* (Hubbs and Hubbs, 1932*b*) we concluded:

> The conditions demonstrated by this study, so far as we know novel in the biology of the vertebrates are: (1) the abundant occurrence in nature of a form of demonstrated hybrid origin, having nearly all of the characteristics of a natural species; (2) the occurrence of a form as females only, over a wide portion of its range [in fact, we now know, over its entire range]; (3) the consistent and abundant production of wholly female and purely matroclinous young; (4) apparent parthenogenesis in nature.

We continued in our genetic test of the complete production of females and the totally matroclinous inheritance of *Mollienisia formosa*. Year after year and generation after generation, unto the twenty-first generation, our *Mollienisia formosa* females continued to produce all-female broods of fish, many hundreds in all, that were replicas of their mothers, although we had mated the mothers with all the available species of *Mollienisia* and with various simple and multiple hybrids between the species of this genus. We mated them with the black mutant of *Mollienisia*, that always throws black-blotched young when crossed with normally colored specimens of *Mollienisia* of the same or other species. We also had broods from matings of *Mollienisia formosa* with species of the related genus *Limia*, though such broods are not often produced. Twice we obtained two young by mating a *Mollienisia formosa* with a male of the mosquitofish, *Gambusia affinis*, belonging to a distinct subfamily. This amazing result, which we could hardly believe, suspecting an experimental error, led us to repeat trial matings of this heterogeneous combination. After several failures we planned and executed a forced mating. We injected a *Gambusia* male and an Amazon molly with pituitary extract to induce rapid and simultaneous maturity. We then injected some sperm stripped from the *Gambusia* into the tiny oviduct of the molly. In due term she gave birth to twelve healthy young, which all grew up into adult females—again just like the mother, with no trace of *Gambusia* characters. But the best characters in these fishes lie in the gonopodium, which is the anal fin of the male highly modified to serve as the intromittent organ. Being females, the offspring of the

outcrossing showed no male characters—until we bathed some of them in the dilution of testosterone that we had found to be effective and thus forced them to develop the secondary male characters. The gonopodium that developed, normally, showed no trace of *Gambusia* characters, but was strictly that of a *Mollienisia*. Furthermore, the colors of the nuptial male of *Mollienisia* became evident.

Always the result was the same—all female young, fully typical of *Mollienisia formosa* in every detail of character, not only in the first generation, but also in subsequent backcrosses and outcrossings. Thus the male used may have had 6, 8, 10, 13, or 17 dorsal rays, but the progeny, modally, had 11 like their mother. Since we have found no trace of such genetic behavior in systematic characters of any other fishes, in this or other groups, and since *formosa* is very fertile, giving birth to full complements of healthy young that often all develop to maturity, we consider the genetic evidence as next to conclusive, that *formosa* transmits to all its offspring only its own maternal chromatin.

*Mollienisia formosa* seems to have arisen as a hybrid, but now has almost all the characteristics of a species. It is completely differentiated from its supposed parental species *latipinna* and *sphenops*, and certainly breeds true, much truer in all probability than most species. It justifies systematic consideration on ecological and historical grounds, which in this case as in general I regard as being quite as significant as the genetic potential: it has increased and spread, for it now occupies a considerable and definite range, including areas where only one of the parental species exists or has likely ever existed. In some places it outnumbers the parental species. The circumstances that its fecundity is high and that 100 percent of its population instead of little more than 50 percent are female breeders would seem to give it a definite selective advantage within the range of the genus, since it mates freely with the males of all species of *Mollienisia* and since the males of poeciliid fishes promiscuously mate with many females. We think it best to treat the Amazon molly as a species, presumably of hybrid origin. This is a special but particularly interesting and significant crossing of the species line.

### *Intermediacy of Hybrids*

In all our work with hybrid fishes in this or any other family, the only taxonomic character that we have been able to attribute to the action of a single gene is the dorsal and anal ray numbers in the subspecies of the mosquitofish, *Gambusia affinis*, (Hubbs and Walker, ms.). The Atlantic Coast form, *G. a. holbrooki*, has 7 dorsal and 10 anal rays, the Mississippi Valley form, *G. a. affinis*, one fewer in each fin (6 dorsal and 9 anal). Intergrades, obviously produced through hybridization near the Gulf of Mexico in Mississippi and Alabama, have either 6 or 7 dorsal rays and either 9 or 10 anal rays. The sum of the ray counts is therefore 17 in the Atlantic Coast form, 15 in the Mississippi Valley form, and 15, 16, or 17 in the intergrades. The intergradation though narrow in area is gradual. First-generation hybrids have 7 dorsal and 10 anal rays, showing that the Atlantic Coast type is completely dominant in this regard. In the $F_2$ generation the condition shown by the intergrades is at once attained, for the dorsal rays are either 6 or 7, the anal rays either 9 or 10. Other characters, however, such as those of the gonopodium and of the sensory pores on the head, remain intermediate and give evidence of being due, like nearly all taxonomic characters, to multiple genes.

It has proved to be an almost universally valid rule that natural interspecific hybrids are intermediate between their parental species in all characters in which those species differ, whether they be external or internal, of shape, color, form, structure, or numbers of parts (vertebrae, gillrakers, fin rays, teeth)—except for some features that reflect hybrid vigor.

This intermediacy has been most extensively analyzed for the numerous hybrids we have described (Hubbs, Hubbs, and Johnson, 1943) in the family of suckers, Catostomidae, from many streams in the western states. Intermediacy is seen in such external characters as the coloration, the general body form, the size of the head, the length and protrusion of the snout, the size of the scales. The lips are definitely transitional in structure. When statistically analyzed the proportions and counts of the hybrids are seen to be not only definitely intermediate, but also of the same order of variability as shown by the parental species—strong evidence that the hybrids are of the sterile $F_1$ generation. The intermediacy may involve the type of relative growth. Internal characters, such as those of the skeleton, may also be transitional. When the values for the hybrids are computed as an index, on a percentage scale grading from the value for one parent, set at 0, to the value for the other, set at 100, the indices form a frequency distribution with the mode very close to 50, which represents ideal interjacency.

The most extensive data that we have analyzed for any one hybrid combination pertain to mass hybridization and species replacement in the Mojave River system. In our published study (Hubbs and Miller, 1942) we reported on 3350 individuals of the species *Gila orcutti*, that we now feel sure was introduced, on 1812 of the native chub, *Siphateles mohavensis*, and on 442 hybrids, constituting 7.9 percent of the entire random sample (or 9 percent if we exclude the fish collected from one spring, into which the introduced species has no access). The hybrid proved on analysis to be intermediate in nearly all characters of color, form, and number of parts. The variable intermediacy extends to such fine characters as are exhibited by the scales. Particularly significant is the intermediacy of the hybrids, with very little overlap on the frequency distribution of either parental species, in the number of gillrakers. The native chub, though confined in Recent times to trickling streams, has very numerous rakers, which were obviously adapted for the straining of plankton in the large lakes that occupied the depressions of the Mojave Desert in Pluvial times. The minnow introduced (as bait) from the coastal streams of southern California has very few rakers, since its diet is essentially the bottom invertebrates, for the consumption of which it has no need for a fine straining apparatus. Data from successive years showed a marked increase in the relative numbers of the introduced species, which seem much better adapted than the relict lake chub to the present-day desert trickles. Collections made in 1953 indicate that the better-adapted introduced species has now almost completely replaced the doomed native form. Hybridization has doubtless co-acted with competition in this rapid replacement of a less well-adapted native species by a better-fitted introduced form.

Although it has long been recognized that interspecific hybridization is a common and important phenomenon in the Plant Kingdom, it has generally been held that in the Animal Kingdom species lines are only rarely, sporadically, and insignificantly crossed. In order to appraise the significance of interspecific hybridization among fishes, we will need to consider for different groups and in different habitats, the extent of such crossing, in terms of the number or proportion of species that cross and, in given combinations, in terms of the number or proportion of hybrid individuals. We also need data on the fertility of the hybrids when intermated, when backcrossed to each of the parental species, and when outcrossed with still others. We also need to know the viability of the hybrids and their chances of survival under different conditions. Some of these numerical relations have been determined; other determinations await much more observational, statistical, and experimental evidence.

### *Marine Fishes*

An extended search by us for natural hybrids, involving the careful examina-

tion of about one million specimens of freshwater fishes and about an equal multitude of marine species, has yielded, along with the results of research by others, some idea of the frequency of hybridization. Two conclusions stand out vividly, (1) that frequency of hybridization, like speciation in general, is to a large degree a function of the environment, and (2) that among marine fishes in general, as contrasted with northern freshwater fishes, hybrids are excessively rare.

The one group of marine fishes in which hybridization is both fairly common and well authenticated is the flatfishes. In Europe there have been discovered hybrids of one interspecific (and intergeneric) combination among the turbots and of four combinations among the right-eyed flounders. One combination, between flounder and plaice, is rather common and has been experimentally produced. Stocks of hybrids of this combination have been planted to test migrations and survivals. Two combinations in the Pleuronectidae have been identified from western North America, and we have analyzed in detail the rather common hybridization of two genera in Japan (Hubbs and Kuronuma, 1942). Hybridization among the flatfishes has been attributed to their life on very uniform sand and mud bottom and to promiscuous mass spawning. Years ago I discovered that two species of silversides (family Atherinidae) living on the sand bottom of the South Atlantic coast hybridize rather frequently, and this case has been analyzed by Gosline (1948).

With these exceptions, hybridization between marine species has been detected or definitely suspected to occur in only a few scattered combinations and with extreme rarity in these few combinations. This is true despite the fact that in cool and more especially in warm seas many closely related species live together. True, much of the study of marine fishes has been less extensive and less intensive than the researches that have led to the recognition of so much crossing of the species in fresh waters, but along the West Coast, from Alaska to Mexico, and to a considerable degree in Japan and on the Atlantic coast of North America, we have done systematic work comparable to that which we have done on the freshwater fishes of North America. The researches we are now undertaking on pelagic and bathypelagic fishes are disclosing no hybrids. Before we attempt an appraisal of this difference in the incidence of hybridization, let us briefly review the evidence on interspecific hybridization in different families of fishes in the fresh waters of North America.

### *Hybrids in Freshwater Fishes*

Among the lampreys (Petromyzontidae) we have moderately conclusive evidence of occasional hybridization between two freshwater species of *Ichthyomyzon* (Hubbs and Trautman, 1937).

Among the trout we find occasional intergeneric hybrids in nature as well as in culture. Most of these are between the native brook trout and the introduced brown trout. In the West the cutthroat and rainbow trouts, both belonging to the genus *Salmo*, live side by side with little or no crossing in many coastal streams, but in the interior, where the cutthroat alone was native, the introduction of rainbows has repeatedly led to very extensive hybridization, and frequently to the elimination of the cutthroat, through a combination of hybridization and superior competition. The rainbow and golden trouts hybridize similarly. In the hatcheries many crosses have been produced between good species of chars, trouts, and salmons. Some of these produce fertile offspring, and by mating one hybrid with one of another cross, four species of the Pacific salmons have been combined in one individual (among the poeciliids we have thus combined as many as five species and twelve subspecies or races). One combination, between the brook trout and the lake trout, is being propagated in Canada with

promise of use in fish management. The parental species were formerly classed as distinct genera, but in the current lumping spree both are put in *Salvelinus* —which action does not lessen the difference between the species.

Hybrids between the whitefish and the lake herring or cisco of the Great Lakes, of the related family Coregonidae, have been found in nature (rarely) and have been experimentally produced (Koelz, 1929). They also represented an intergeneric cross a few years ago, but only an interspecific cross now, owing to the revised generic delimitations—a subjective matter. I have interpreted other specimens as interspecific hybrids within the subgenus *Leucichthys*.

Attention has already been given to hybridization in the suckers (Catostomidae), with reference to the characters of the hybrids, but we need to indicate the frequency of hybridization and its relation to the phylogeny of the group. In our first and most comprehensive study (Hubbs, Hubbs, and Johnson, 1943), we identified from the Western states 182 interspecific hybrids representing nine interspecific and in part intergeneric combinations. The 182 hybrids were 11.5 percent as numerous as one parental species taken in the same collections and 7.2 percent as numerous as the other parental species. In terms of all specimens examined from the same river system, the hybrids were 1.8 percent as numerous as one parental species, 1.5 percent as many as the other. In some crosses the hybrid ratio was higher; in one intergeneric cross in the Columbia River system the ratios of hybrids to the two parental species were 15.1 and 21.6 percent for collections containing hybrids, and 6.4 and 4.2 percent for all specimens known from the entire river system. Owing to the mass collecting technique of modern times there has been little selection of hybrid specimens in the field. It seems safe to conclude now, as it was when we published the main paper, that among the suckers in all the lakes and streams of the Western states at least one in a hundred is an interspecific hybrid. Conditions conducive to hybridization include the association of a few individuals of one species with an abundance of another, and the introduction of one species into the natural range of another. When thus thrown together, types that avoid hybridizing, where they occur together naturally, will cross. Subsequent studies (Hubbs and Hubbs, 1947; Hubbs and Miller, 1953; and ms.) have confirmed and expanded the conclusions reached in the paper cited.

For the suckers, and for several other freshwater fish families of North America, charts (Figs. 1 to 8) have been prepared to show by white rectangles the combinations of which no species occur in the same region, and hence cannot be expected to hybridize in nature; by gray rectangles, those that do occur together, but are not yet known to include hybrids; and by black rectangles, the combinations that include, to the best of our knowledge or judgment, at least one interspecific hybrid. Each such entry may represent several different interspecific combinations; of each combination we may have studied many series of specimens, and the total number of specimens may run into dozens or even hundreds. The recognized subfamilies are separated by heavy lines and the tribes by medium-weight lines. The genera are in full capitals; the subgenera, bracketed together, in lower case. The sequence is intended to be phylogenetic (in so far as may be indicated by a single column), so that combinations among most closely related generic groups should cluster along the diagonal, along which lie the combinations within each of the charted units. Note that for the Catostomidae (Fig. 1) the known hybrids are confined to tribal limits. All of the many sucker hybrids already discussed belong in the one tribe Catostomini. The other hybrid suckers that have been observed are between two buffalofishes (subfamily Ictiobinae).

The largest number of hybrid combina-

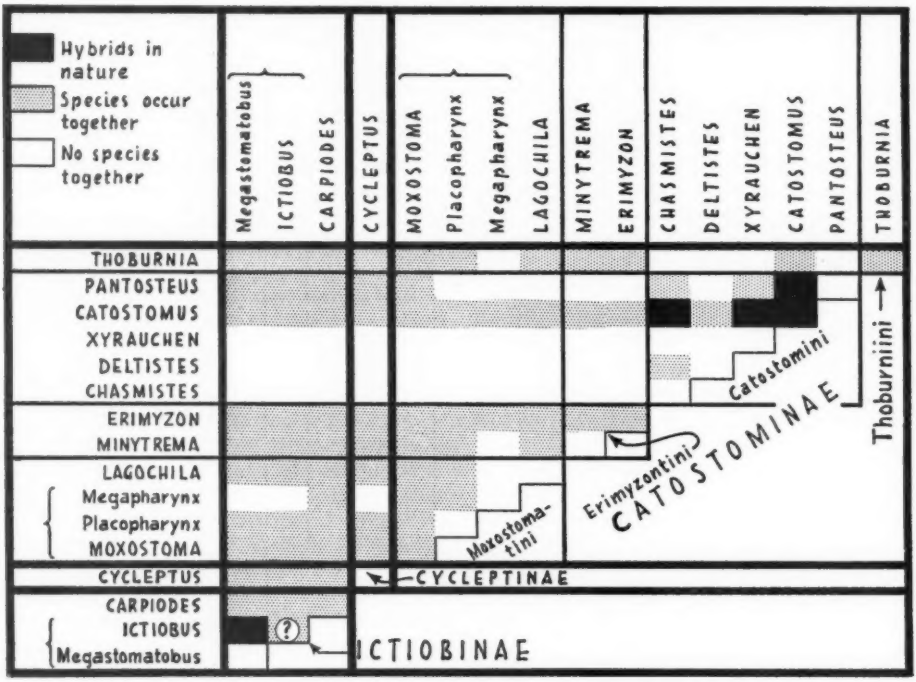
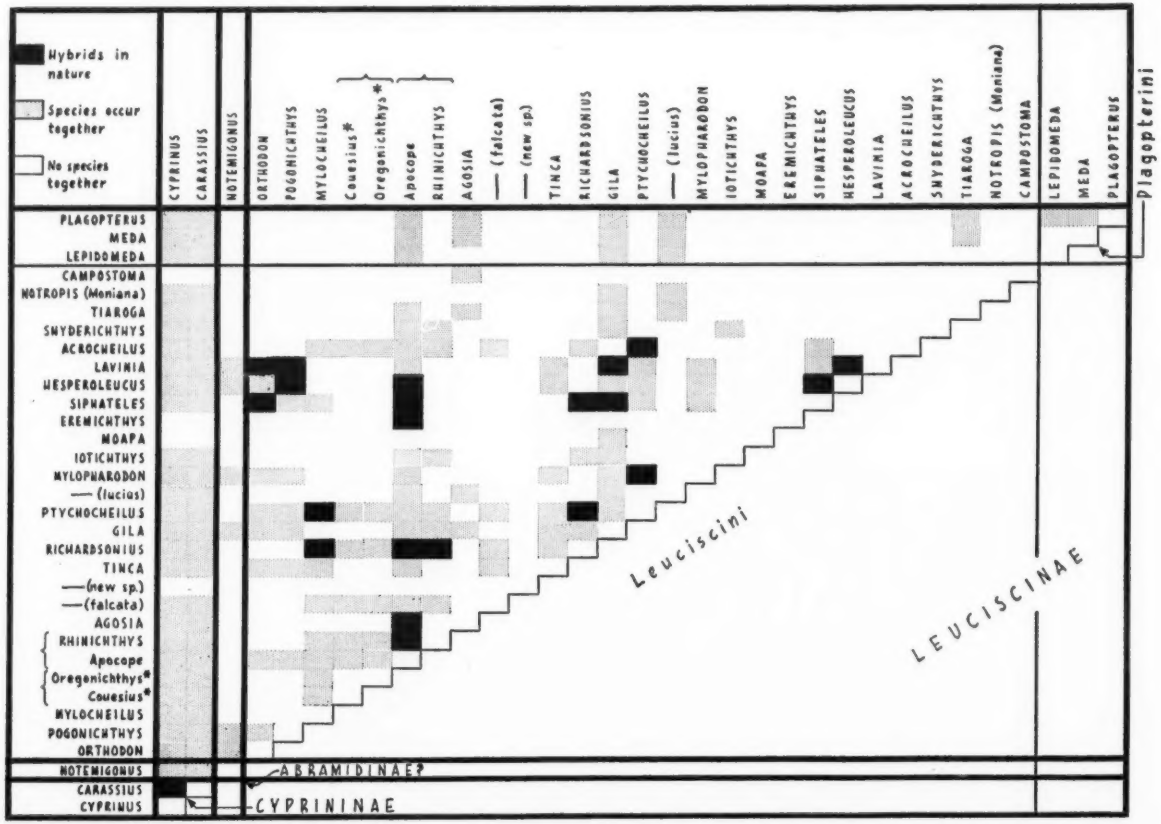



FIG. 1. Classification of North American Catostomidae, with indication of recognized hybrids between subgenera (printed in lower case) and genera.

tions occurs in the Cyprinidae, which is by far the most speciose family of North American freshwater fishes. The subgenera and genera of minnows are so numerous that we are forced to set up separate diagrams for the Pacific and Atlantic slopes. Taking the chart for the western slope (Fig. 2), we note first (at the lower left) hybridization between the carp and the goldfish in the subfamily Cyprininae. This cross has been produced in captivity and occurs very commonly in the East, especially about Lake Erie, where goldfish that escaped in a storm from a rearing pond got into Lake Erie, multiplied, and started interbreeding with the carp, previously established. The hybrids have become rather abundant locally. In one small creek in Ohio we found that the physiologically active hybrids had sorted themselves out, as sunfish hybrids sometimes do, so that, locally, they greatly outnumbered the parental species combined. In their native home, in eastern Asia, the two genera live together with little or no miscegenation, though they have been crossed there in captivity. Seemingly because of separation for a few decades or centuries, the two types have lost the art of avoiding the wasteful practice of producing sterile offspring (the uniformly intermediate characters of the hybrids indicate sterility). The carp-goldfish hybrids are uniformly intermediate, with about the same variation as each parental species. They are being reared for sale as bait, as they grow rapidly, are very hardy, and, being sterile, will not become established when bait is released.

The other hybrids among western cyprinid fishes involve crosses between rather diverse genera. In certain waters




*Subgenera of Hybopsis

FIG. 2. Classification of the Cyprinidae of the Pacific slope north of Mexico, with indication of recognized hybrids between subgenera (printed in lower case) and genera (omitting *Tinca*, an introduced genus not known to hybridize with other genera).

most of the genera hybridize with one another in different combinations, sometimes rather commonly so. In one rather isolated stretch of the San Juan River of the Salinas system the genera *Hesperoleucus* and *Lavinia*, like certain plant species, have crossed to produce a hybrid swarm, involving almost the entire population and, locally, breaking down completely the bars between the species. Because of the sharp differentiation of the Western freshwater fish faunas, a large proportion of the genera and subgenera do not cohabit. Of the 120 pairs that do occur together, 17 percent have already been found to produce hybrids in nature. Three more of the combinations produce hybrids on the Atlantic slope.

In the chart for the Atlantic drainage (Fig. 3) we have omitted the Cyprininae, containing the carp and the goldfish and their numerous hybrids, already discussed, and three other exotic genera that are not known to hybridize in any way. For some unknown reason, the golden shiner, *Notemigonus*, seems to be immune to crossing on either slope. In the East a much higher percentage of the generic groups live together and hybridization is scattered throughout the series of native fishes. Formerly these minnows were placed in several subfamilies, but I am now inclined to class them in a single subfamily, even in a single tribe (Leuciscini). The apparent freedom of crossing is one reason for this changed evaluation. The record would seem to indicate that the cyprinids did not populate America prior to the Miocene and that at most a few immigrants have through radiative adaptation erupted into the very rich Recent fauna. Hybridization has remained, or has become very widespread. The very highly aberrant genus *Campostoma*, with the intestine wound spirally around the gasbladder, crosses with seven other genera. The subgenus *Luxilus* of the very speciose genus *Notropis*, containing the common shiner *Notropis cornuta*, hybridizes with fourteen other subgenera and genera. Of the 608 pairs of subgenera and genera that live together, 68 (11 percent) have hybridized in nature, according to our best evidence. The interspecific combinations are more frequent than the subgeneric in number, of course, but not proportionwise. The chart of hybridization has grown with the years, until most of the major areas of possible hybrids have received at least one entry. It has been like filling in the periodic system of the elements.

Hybridization in the minnows has been attributed largely to the chance meeting of sperm and egg. As many as six or more species may be seen breeding violently on a single small gravel patch, commonly the nest of a large species. Very frequently *Notropis rubella* spawns in midwater a few inches above *Notropis cornuta*, which spawns on the bottom. The hybrids between these two species are perhaps the most commonly taken of any combination. The actual nuptial embrace of one species by another has not been observed, but is unnecessary to explain the frequent hybridization. Since the hybrids between *Notropis rubella* and *N. cornuta* appear to bridge the gap between the two species and have a normal sex ratio, it is assumed that they are at least partially fertile. The numerous hybrids between *Chrosomus eos* and *Chrosomus neogaeus* (formerly *Pfrille neogaea*) are invariably or almost invariably female.

Among the North American freshwater catfishes, the Ameiuridae, the few known hybrids are between species of *Ameiurus* and between species of *Schilbeodes* (Trautman, 1948; W. R. Taylor, ms.). A close connection between hybridization and classification is again indicated. In the South American catfish family Pimelodidae I have found a few hybrids between two species of *Rhamdia* in Guatemala.

In the pike family Esocidae (with one genus *Esox*) hybridization is rather common in nature and has been checked experimentally, but only the species of adjacent size seem to cross: the 10-inch

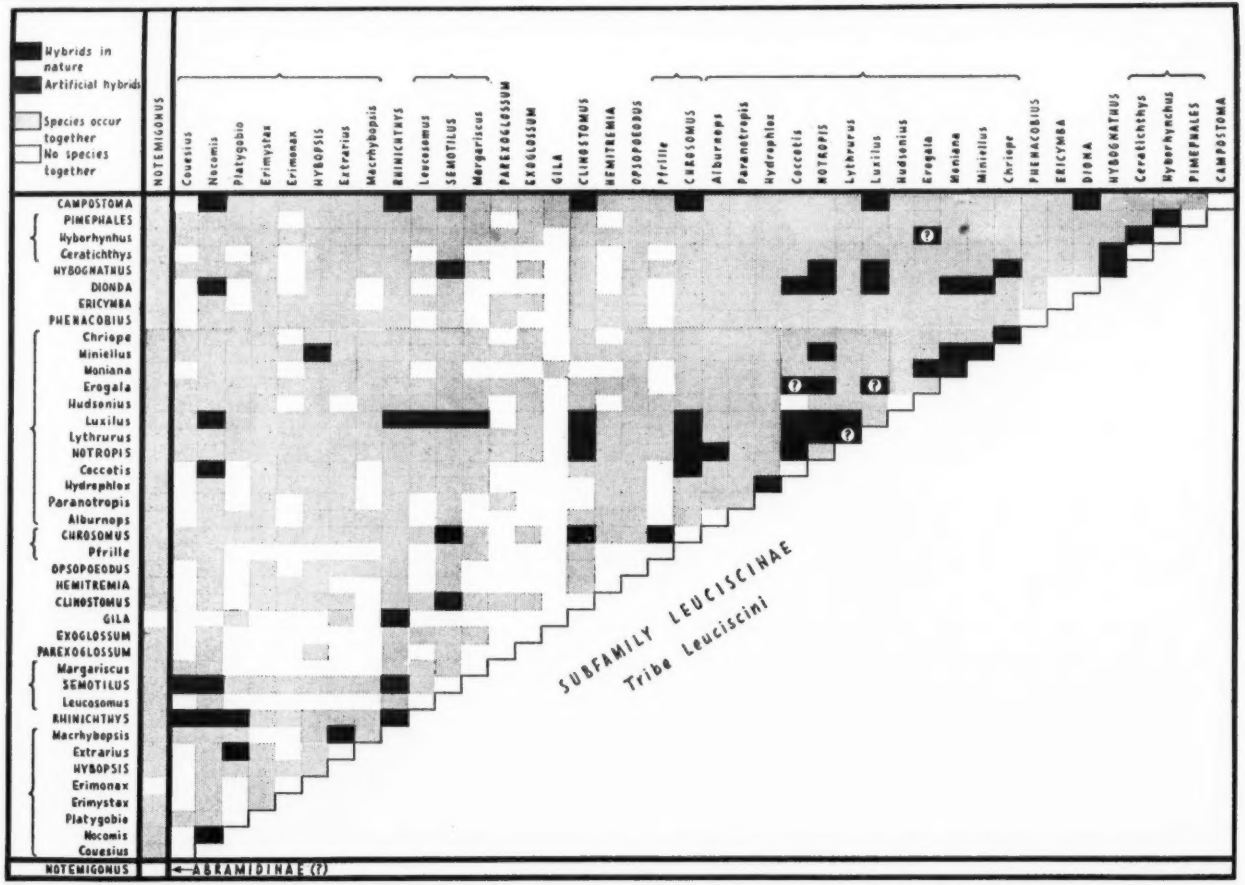



FIG. 3. Classification of the Cyprinidae of the Atlantic slope north of Mexico, with indication of recognized hybrids between subgenera (printed in lower case) and genera (omitting the Cyprininae, which are included on Fig. 2, and three genera, *Tinca*, *Scardinius*, and *Rhodeus*, that are not known to hybridize in North America).

bulldog pickerel (*americanus*) with the 18-inch chain pickerel (*niger*); the chain pickerel with the 3-foot northern pike (*lucius*); and the pike with the 5-foot muskellunge (*masquinongy*). The last-named cross has received some attention in fish culture (Eddy, 1944; Black and Williamson, 1947, with other citations).

Among the killifishes, or oviparous cyprinodonts (Fig. 4), a few of which range into brackish or even salt water, three interspecific combinations are known, all within the primitive tribe Fundulini (Hubbs, Walker, and Johnson, 1943). Hybridization in this group seems to be conditioned by cohabitation of a few individuals of one species with an abundance of the other.

Among the viviparous cyprinodonts two species of the Mexican family Goodeidae, regarded as generically distinct though closely related, have been found to hybridize rather commonly (Hubbs and Turner, 1939).

In the larger and more widespread, exclusively American family Poeciliidae very few natural hybrids are known, though members of this family have been more extensively hybridized than any other in home aquaria and in genetic laboratories. One reason seems to be that this group has a very wide range, from central United States to Argentina, so that many of the genera are of such limited range that they occur with few others, some with no other. Another reason is that copulation in this group follows complex nuptial performances, often characteristic of genera. In the large subfamily Gambusiinae (Fig. 5) very few hybrids have been identified, representing two subgeneric crosses in the mosquitofish

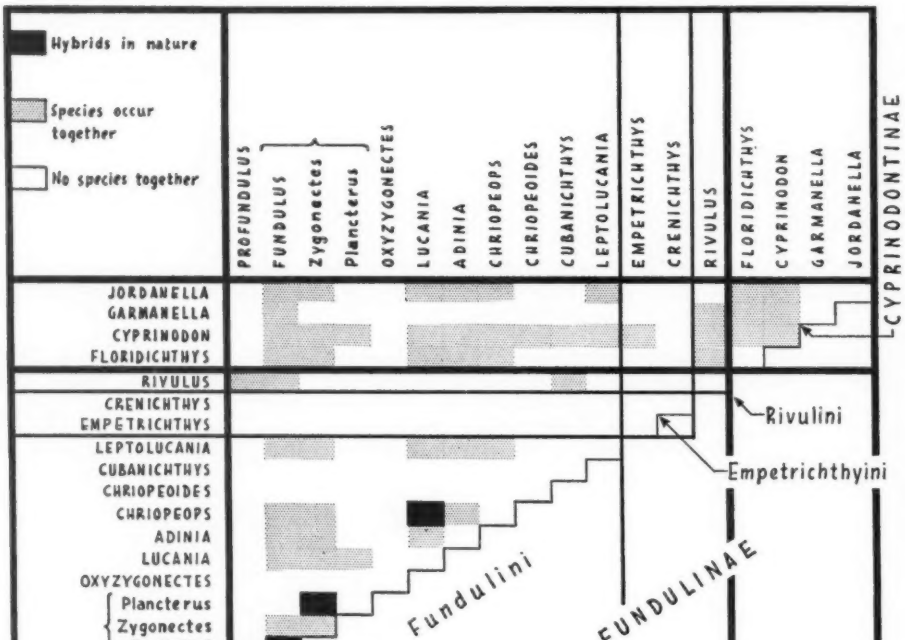



FIG. 4. Classification of the Cyprinodontidae of North America, with indication of recognized hybrids between subgenera and genera.

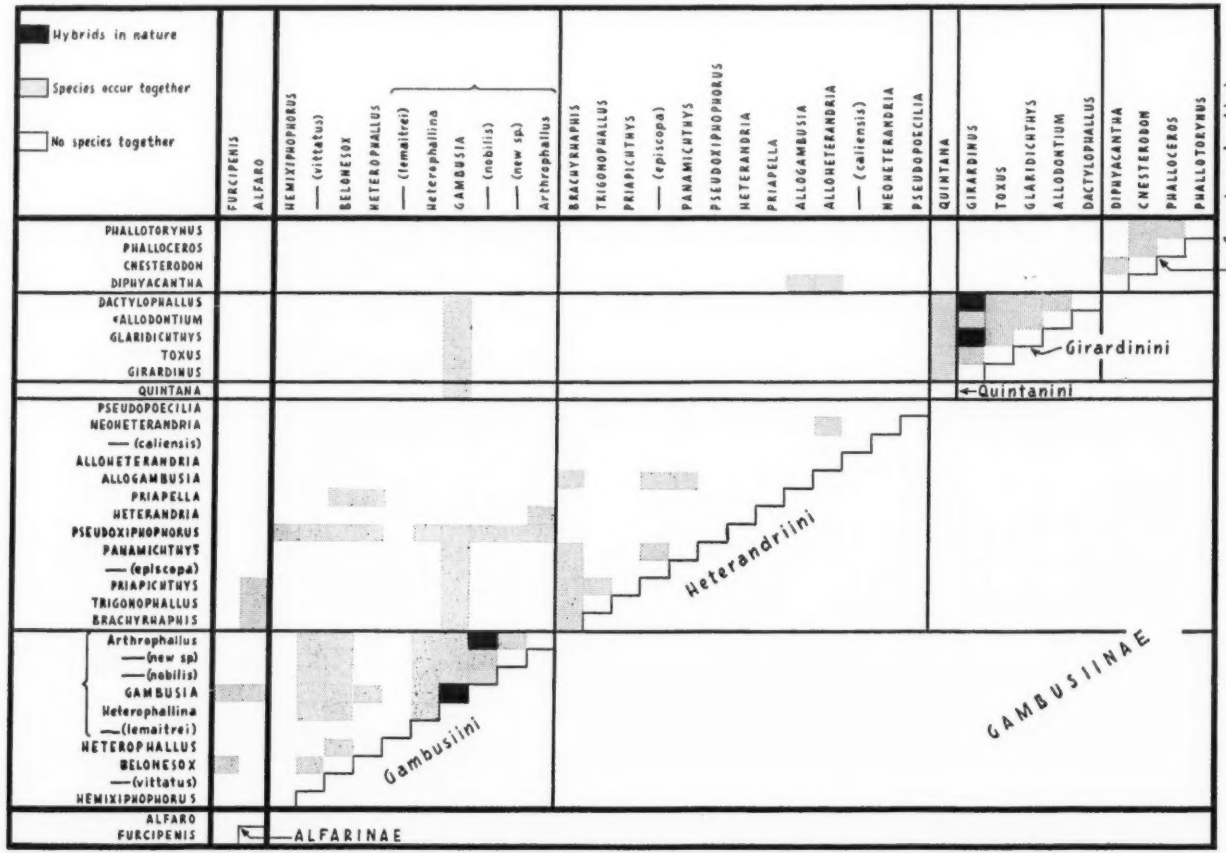



FIG. 5. Classification of the Poeciliidae of the subfamilies Alfarinae and Gambusiinae, with indication of recognized hybrids between subgenera and genera.

genus *Gambusia* and two intergeneric combinations in the Cuban tribe Girardinini (Hubbs and Rivas, ms.).

In the subfamilies Poeciliopsinae and Poeciliinae, also, very few natural hybrids are known (Fig. 6). Dr. Robert Rush Miller, however, has found considerable hybridization between certain species of *Poeciliopsis*. In the tribe Xiphophorini no natural hybrid has yet been identified, though all species seem to be crossable in aquaria and most combinations have been effected. The very extensive genetic work by Gordon, Kosswig, and others has been done in this tribe, with crosses between the various species of swordtails and platies (all now classified in the genus *Xiphophorus*).

In the tribe Poeciliini we have found in nature a very few natural hybrids between species of *Mollienisia*, in Yucatan (Hubbs, 1936), Guatemala, and Hawaii (a different interspecific combination in each country). In Hawaii, where both genera were introduced, I have also found hybrids between the related genera *Limia* and *Mollienisia*. Crosses between *Lebistes* and *Mollienisia* have been made in home aquaria and have been verified by me. Various other crosses have often been claimed, as between *Lebistes* and *Xiphophorus*, but every such supposed intertribal cross that I have checked has proved to be referable to one or the other of the alleged parental species.

Probable hybrids of one combination have been reported in the freshwater Atherinidae (Jordan and Hubbs, 1919, p. 77).

In the perch family (Percidae) we find again a close correlation between hybridization and classification (Fig. 7). The

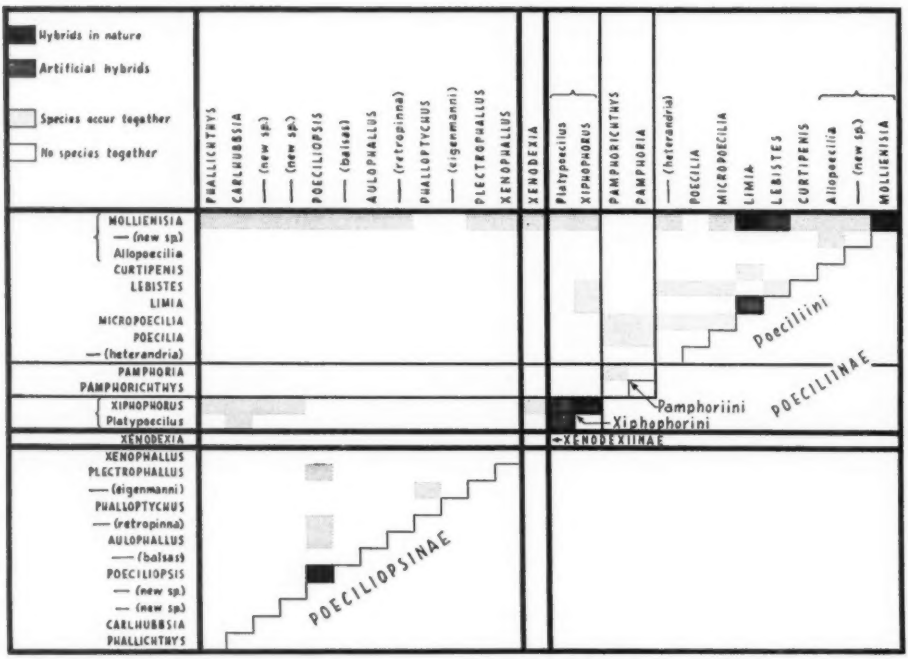



FIG. 6. Classification of the Poeciliidae of the subfamilies Poeciliopsinae, Xenodexiinae, and Poeciliinae, with indication of known experimental and natural hybrids between subgenera and genera.

FIG. 7. Classification of the North American Percidae, with indication of known experimental and natural hybrids between subgenera and genera.

yellow perch, representing the Percinae, does not hybridize with any other fish. The two main species of the Luciopercinae hybridize occassionally, and the yellow and the blue walleye appear to cross so often that they are now treated as subspecies (the decision is in part arbitrary). No member of the Luciopercinae hybridizes, so far as is known, with any genus in either of the other subfamilies.

In the subfamily Etheostomatinae, the diminutive perches known as "darters," hybridization is moderately common but in nature is restricted largely to the less reduced and more primitive genera and subgenera. A few hybrids are known to occur between several species among the smaller and more brilliant, specialized darters, within a subgenus or between closely related subgenera. Among the thousands of specimens examined by me, only two represent natural crosses between the more primitive and the more specialized genera. Several laboratory crosses are being made by Clark Hubbs and by Allan Linder, with rather ready success among the highly specialized darters, but in general with poor success in crosses between the primitive and the specialized genera. Here again is evidence of a close correlation between hybridization and relationship. Crossing of the species line in this family as in the minnows may well result from the chance meeting of eggs and sperm when two species breed in close proximity, as they often do.

In the sunfish family Centrarchidae (Fig. 8), as well, hybridization is confined to the limits of single tribes. We have found several hybrids between species of blackbass, but only in the subgenus *Micropterus* (Hubbs and Bailey, 1940). Within the sunfish tribe Lepomini, comprising nine genera as recently classified but only two at present, by reason of lumping, 18 (about one-half) of the 38 possible subgeneric crossings have already

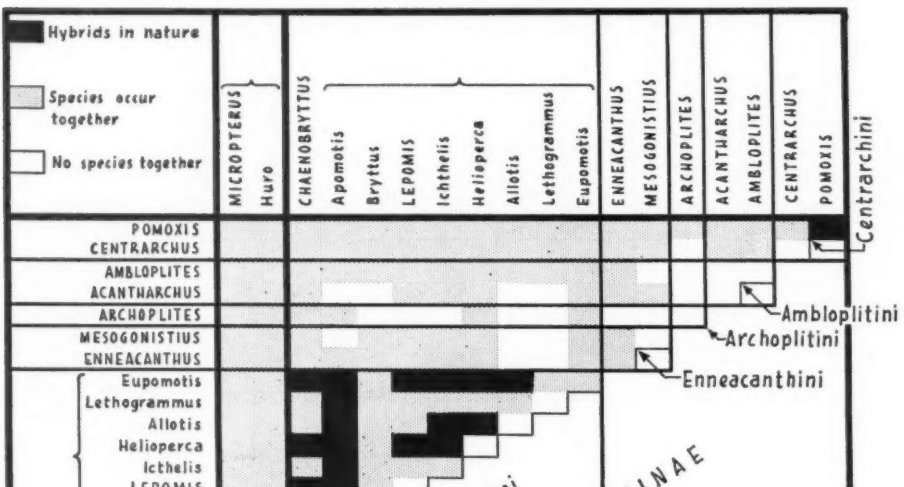



FIG. 8. Classification of the Centrarchidae, with indication of recognized hybrids between subgenera and genera.

been realized. The main features of the abundant hybridization in this tribe have already been outlined. The other interspecific hybrids in the family are between the two species of *Pomoxis*, in another tribe.

The only other natural hybrid recognized in the fresh waters of North America is between two species of sculpins, of the genus *Cottus*, and this cross needs further study.

The frequent crossing of the species line in the freshwater fish fauna of eastern North America is duplicated in Europe in the minnow and trout families (where it would be expected). A few minnow hybrids have been reported from Asia and some of the Indian cyprinids have hybridized in aquaria. In Africa and South America, at least some interspecific hybridization can be predicted, though it has seldom been indicated. It is not at all improbable that hybrids in those continents have been studied and named as distinct species, just as the sunfish hybrids were in North America before they came under close scrutiny.

It would be of particular interest to determine whether and to what degree the species lines are crossed in the large lakes, especially the rift lakes of Africa, where radiative speciation has dramatically exploded, to produce rapidly, with very little geographic isolation, a great number of species. Under such conditions I would expect much crossing of the line between the recently differentiated species. Dr. Ethelwynn Trewavas of the British Museum has told me that she has reason to suspect that some of the variants and some of the nominal species encountered in the study of the extraordinarily numerous cichlid species of the African lakes may be interspecific hybrids. In critically examining Dr. Tchernavin's report on the multitudinous species of the cyprinodont genus *Orestias*, endemic in Lake Titicaca, Perú, I found evidence of some interspecific hybridization, and in treating the atherine genus *Chirostoma*, which has proliferated extensively in the lakes of the Río Lerma system of México, Jordan and Hubbs (1919, p. 31) discussed three probable interspecific hybrids of one combination.

### *The Role of Environmental Factors*

Even if no further evidence of interspecific crossing among freshwater fishes should be discovered, the conclusion would stand out boldly that such hybridization is vastly more common in fresh waters than in the sea. This contrast cannot be attributed solely to a difference in the genetic potential of families respectively more or less confined to fresh and ocean waters, for the hybridization occurs in all of the larger families in North American fresh waters, including some families that have close relatives in the sea.

It is evident that the hybridization is conditioned by environmental factors. Some of these factors have already been indicated. Species that rarely or never hybridize in nature can often be crossed, sometimes very freely, in captivity. Merely placing a male of one species with a female of another in an aquarium may lead to crossing. Thousands of such matings between the swordtails and the platies have been consummated, yet not a single hybrid between the two has ever been taken in nature, despite the fact that they often occur together and have been very extensively collected and very critically studied. Species of *Mollienisia* that hybridize in nature with extreme infrequency cross very freely in aquaria, in some combinations with no decrease in fecundity in the first or even in the succeeding generations. Many combinations that seldom or never cross voluntarily, even in planned matings within the confines of an aquarium, prove their basic genetic compatibility when the breeders have been injected with hormones, or when artificial impregnation is practiced. The genetic potential often remains unrealized.

Similarly, where the spawning areas in

nature are greatly limited and the breeding fish are thus forced into close proximity, the incidence of hybridization is increased. Spawning in proximity may lead to the chance meeting of eggs and sperm, but may also lead to the mating of species that breed with complex pairing behavior. The cohabitation of a few individuals of one species with a multitude of a related species is another circumstance definitely conducive to crossing, especially when the scarcer species has been introduced. When ready to spawn, the species that is locally rare may outcross if the proper mates are not at hand. As in plants, hybridization is often a function of the intergradation of the habitat: species that are segregated in breeding by differential responses to any features of the physical, chemical, or organic environment tend to breed together where the environment is rendered intermediate, either through natural causes or through modifications by man. And species that normally breed at different seasons may cross where conditions are such as to cause an overlap in the breeding seasons.

In the light of these thoughts, how can we explain the high incidence of hybridization in the fresh waters of North America (and of Europe), in contrast to the infrequent breakdown of species lines in the sea? We attribute the frequent hybridization in the fresh waters in part to the greater opportunity for chance meeting of egg and sperm, but, more especially, to the ephemeral and changing nature of the environment. Lakes are temporary, often suddenly formed but all doomed to eventual extinction. Most lakes, of limited area and depth, are very transient. As they change in character and approach extinction the habitats are altered or destroyed. Streams also change in character in glaciated areas. In North America and Europe the almost catastrophic changes in climate through the Ice Age, modifying conditions and forcing dispersals, vastly decreased the long-term stability of the ecological niches, and it is in the regions affected sharply by Pleistocene stresses that hybridization has been encountered most often. In North American fresh waters, where hybridization has probably been most frequent, most of the existing fish fauna, furthermore, appears to date only from invasions during the Miocene, Pliocene, and Pleistocene, leaving no very great time for full adjustments. In addition, most freshwater fishes are so limited in possible movements that they cannot reach the full assortment of habitats that might otherwise be available.

In the sea, in contrast, and to a large degree perhaps in more nearly equatorial fresh waters, speciation has had a longer play. Local changes in both time and space may be rapid and profound, but the various ecological niches to which related species have become differentially adjusted remain available, if not in the immediate vicinity, at least within reach along the much freer highways of dispersal. The organic environment has apparently also remained more stable. Much greater opportunities have existed for the development and operation of the multitudinous fine adjustments involved in the location, with precise timing, of the proper breeding grounds and the proper mates.

Contrast in the regional incidence of hybridization may probably be drawn not only between fresh waters and the sea, but also between the temperate regions and the tropical. The environmental and particularly the organismal diversity of tropical regions seems to have been accompanied by very little interspecific crossing (though, as already noted, more critical and complete systematic studies may well disclose some hybridization in tropical fresh waters, and possibly even in tropical seas). The seeming lack of hybridization in the swarming reef fauna of the Indo-Pacific region is amazing. The fact that most of the few marine fish hybrids thus far recognized have come from temperate northern waters may be due not only to more complete studies there, but also to faunal disruptions induced to

some extent in the littoral waters, as well as in fresh waters, by the vast shifts in Pleistocene climate. I venture to predict that the incidence of natural hybridization between species will show a clinal gradation from north temperate to tropical zones, as well as from fresh waters to the sea, with the highest frequency in Holarctic freshwater regions strongly affected by Pleistocene events and the lowest incidence in tropical marine waters. North temperate marine and tropical freshwater fishes may show an intermediate and rather low incidence. Similar relations may well hold for other groups of animals.

Selective advantage as well as conditions imposed more directly by the environment may help to explain not only the general avoidance of hybridization that I have attributed to environmental stability, but also the relatively frequent crossing of the species that seems to be a result of environmental instability. The general avoidance of crossing, where environmental stability permits, seems to be attributable not only to reduced fertility of the hybrids, but also to the selective advantage of the fine adjustments, between species and environmental niches, that can be attained only with relatively uniform genetic constitution. But where the environment is in a state of flux, increased premium may be inherent in the genetic variability that hybridization produces. Material is then needed for new adjustments to the rapidly changing environment. Under these conditions the advantages of genetic variability may outweigh the advantages of uniform constitution. Under more stable environments these opposing advantages may be reversed.

Frequency of hybridization appears to be inversely correlated with the number of species in given areas. It is certainly true in the Catostomidae (the suckers) and I believe also in the Cyprinidae (the minnows) that hybridization is more frequent in the fresh waters of western North America than in the more speciose waters of eastern North America. In the abounding fauna of the tropics many more species come in contact with one another, yet hybridization seems least common. One reason may be that the diversity lies largely in the organismal environment, under which conditions species recognition and specialized reproductive responses and behavior are presumably enhanced (the highly diverse species-specific coloration of tropical reef fishes comes to mind in this connection).

The absence or scarcity of hybridization where species are most numerous is one of several lines of evidence that belittle interspecific hybridization as an important factor in the speciation of fishes. The frequent if not usual sterility or partial sterility of the hybrids is another of the lines of evidence. There is a considerable body of circumstantial evidence, however, to indicate that in at least some groups of fishes in certain regions the crossing of the species line has been a factor of some significance in speciation, particularly in the way of introgressive hybridization.

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# Population Variation and Hybridization in Some Californian Shrews

ROBERT L. RUDD

STUDY of the dynamics of single populations depends essentially on ecological and genetic data. Analysis of the process of differentiation, in essence comparative dynamics of natural populations, demands in addition good knowledge of geographic distribution, morphological variation, statistical methodology, and nomenclatorial practices. By the appropriate application of data from these varied sources, we should be able to examine discrete populations closely and to render satisfactory judgments on their probable origins, on the genetic and environmental factors influencing the pattern of differentiation, and on the present relationships of similar populations. It is a truism to observe that many workers are unable to approach such an ideal with conventional comparative techniques.

A rewarding approach to the analysis of morphological variation in similar forms is available from recent botanical investigations (Anderson, 1949; 1953). The technique consists of simultaneous presentation of several morphological variables using graphical or semigraphical methods. Symbols of various types are used to represent the variable characters. Index values expressing estimated degree of deviation from an established standard may be used as a basis for symbols. The completed "pictorialized scatter diagram" (Anderson, 1949) serves to demonstrate the range of population variation for all figured characters, the extent of introgressive hybridization, and the probable relative position of the putative parental stock of a hybrid population.

The "Andersonian" technique described above has been employed in the analysis of several shrew populations in which standard statistical and nomenclatorial methods have failed to demonstrate properly their characteristics and relationships. Graphic analysis of variation in mammals has been undertaken previously. Symbols on background maps have been used by Blair (1953) in *Peromyscus maniculatus* and Burt (1954) in *Neofiber alleni*. McCarley (1954) used the pictorialized scatter diagram to demonstrate hybridization between *Peromyscus leucopus* and *P. gossypinus*. A type of diagram similar to that of McCarley is used in this paper not only to describe presumed hybrids but also to characterize population types.

### *Study Material*

Two hundred and thirty-five specimens of three species of shrews from the area described have been used critically in this study. Only specimens for which full collecting information was recorded have been used in comparisons. Variations arising from growth and secondary sexual influence have been taken into account. No individuals younger than four months or older than twelve months have been employed (method of age estimation from Rudd, 1955). The majority of specimens are winter-taken and fall in the four- to eight-months age group. Attempts to produce hybrids under artificial conditions were unsuccessful (Rudd, 1953).

The forms in question are recognized taxonomically as *Sorex ornatus californicus*, *S. sinuosus*, and *S. vagrans vagrans*. The ornate shrew (*S. ornatus*) is found

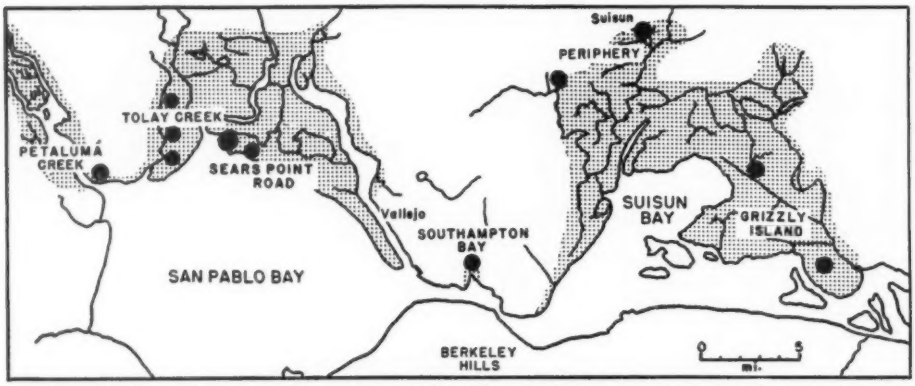


FIG. 1. Map of the marshes under study. The shaded area represents the approximate total area of marsh. Much of the included area is drained and cultivated. The extent of marsh about Southampton Bay is exaggerated. Black dots represent collecting stations.

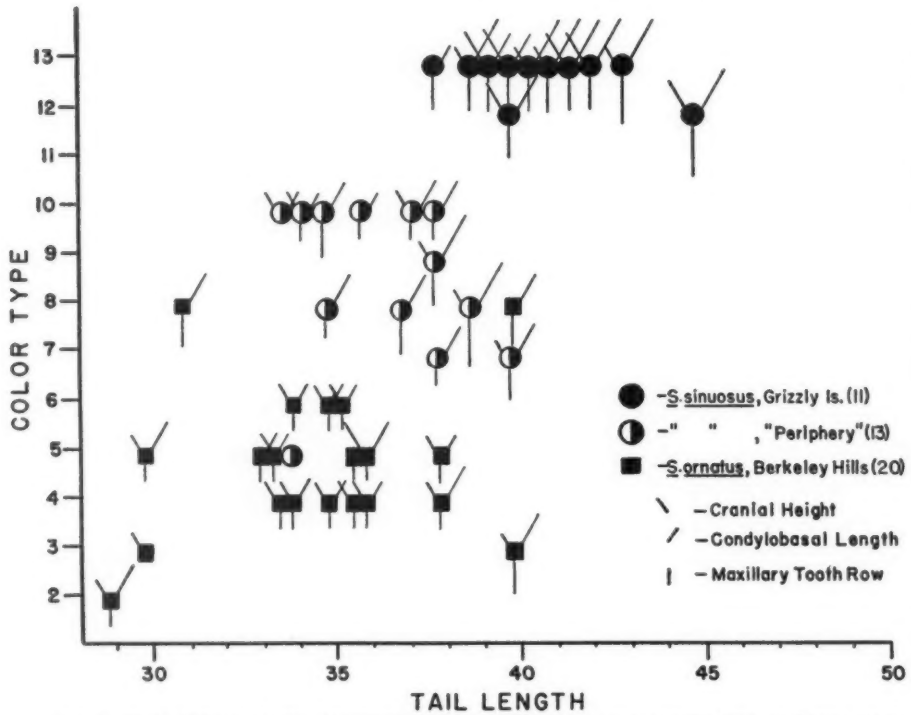


FIG. 2. Pictorialized scatter diagram of individuals from two populations of *Sorex sinuosus* and one of *S. ornatus*. The color gradient is explained in text. Index values of metric characters (applicable to all succeeding scatter diagrams and cumulative indices) were assigned in the following manner. The measurement range of single characters in all the populations was divided into four equal parts. Measurements in the lowest quartile received an index value of "0"; those in the second quartile, a value of "1"; and so on. Precise ranges for these values are given in Table II. An index value of "1" was plotted as a line three-sixteenths of an inch long in the original scatter diagrams.

from the tip of Lower California to the northern Sacramento Valley. It reaches its northernmost point of distribution coastally in the San Francisco Bay region. In general, it favors semi-arid, upland environments although it is also found in fresh- and salt-water marshes. *Sorex vagrans vagrans* extends about a thousand miles northward from the Golden Gate. It is an abundant mammal in humid coastal and montane marshes from Marin County, California, to southwestern British Columbia. The Suisun shrew (*S. sinuosus*) was thought to be confined to restricted marshlands—insular because of large tidal sloughs—on the north shore of Suisun Bay. Quite recently, isolated populations referable to this species have been found in nearby tidal marshes.

*Study Area*

With the exception of the "typical" population of *S. ornatus* all of the described populations lie within the bounds shown in Figure 1. The *ornatus* sample comes from the Berkeley Hills on the eastern margin of San Francisco Bay. The remaining populations divide topographically into three units. The brackish-water, Suisun marshes are surrounded on the east, north, and west by low, grass-covered hills. Portions of these hills are now in pasture or urbanized. Originally, as now, the area was ecologically unsuitable for large populations of shrews. To the south the marshes front Suisun Bay. No contact with shrew populations on the opposite side of this Bay is possible. The

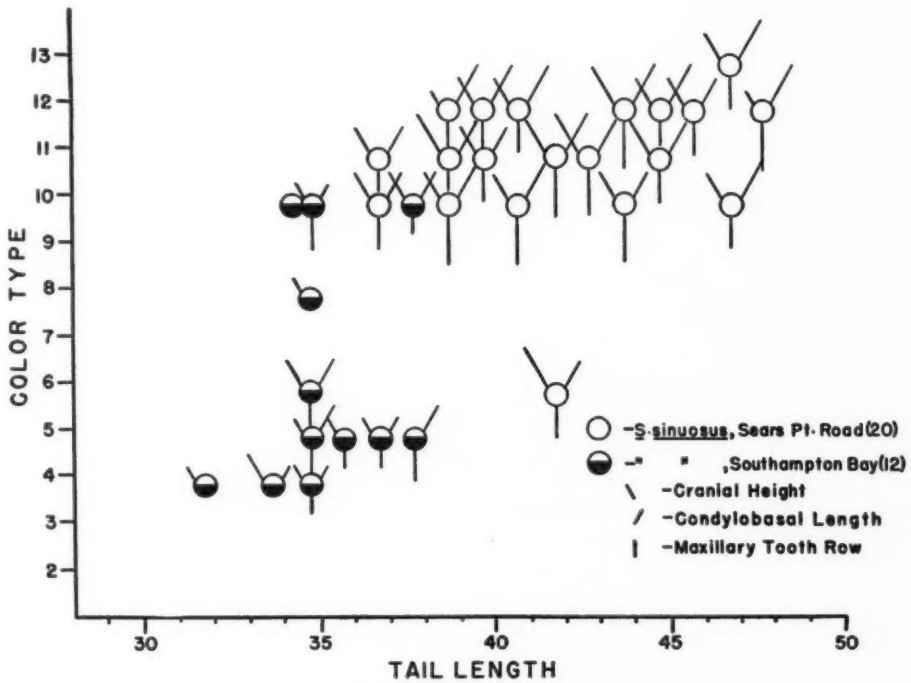


FIG. 3. Pictorialized scatter diagram of individuals from two populations of *Sorex sinuosus*. This figure is to be compared with Figure 2. See Figure 2 and Table II for method of preparing graph.

second unit is Southampton Bay, a short distance from the Suisun marshes but isolated in the same manner. The tidal marsh here is small and marginal (extent of marsh exaggerated in Figure 1). The third unit includes three populations on the north shore of San Pablo Bay. The same hills described above flank it on the east. Low hills covered with oak-grassland mark the western boundary. Between these points exists an environmental continuum broken only by small streams.

In all areas the marsh vegetation is physically much the same. With the exception of the center of the Suisun marshes the vegetation reflects the frequency of tidal inundation. Three plant types are dominant in salt marshes—*Spartina foliosa*, *Salicornia ambigua*, and *Grindelia cuneifolia*, in order of decreasing tolerance to inundation. These plants are present in the brackish Suisun marshes but are dominated by *Scirpus californicus* and *Typha latifolia*. Growth form, not species, of vegetation is the determinant of shrew occupancy. Shrews require a dense, low-lying cover providing an abundant invertebrate food supply. In general, the tidal marsh environment is simple and uniform at equivalent tidal levels.

### *The Populations of* Sorex sinuosus

Four populations of the Suisun shrew may be recognized. Each, populationwise, is readily separable from the other. The most marked deviate is found on the islands in the Suisun marshes. In Figure 2 this population is referred to as "Grizzly Island" from the name of the largest island. The population referred to as "Periphery" includes two localities on the edge of the marsh near the city of Suisun. The Southampton Bay locality has already been described. The fourth population, "Sears Point Road," includes two collecting localities, six and eight miles northwest of the city of Vallejo.

Seventeen measurements and ratios were originally employed in the analysis of these and other shrew populations. Most of these values, although useful for describing individual population parameters, showed limited utility in the comparison of populations. Five values seemed best able to separate this complex of types. The measured characters are tail length, condylobasal length, cranial height, and maxillary tooth row. The only non-metric character is color type. The color gradient as used here requires explanation. A scale of thirteen types is used as the ordinate in Figures 2 and 3. Specimens were selected as types from all available examples of the *ornatus* group in the San Francisco Bay region. Types were arranged in a gradient from least to most melanin deposition. In other words, Type 1 represents the lightest-colored animal, Type 13 the darkest. Color evaluations were made from the mid-dorsal area. Patterns produced by light-colored tips of hairs were considered secondarily.

*The reference population,* Sorex ornatus.

The Suisun shrew was considered by the describer (Grinnell, 1913) to be related to the *ornatus* group. The latest monographer of the genus *Sorex* (Jackson, 1928) concurred with Grinnell in this opinion. Comparison with a "type" population of this species seems warranted. In this instance, the population chosen was that immediately to the southwest of the Grizzly Island population from which it is separated by Suisun Bay. Adequate specimens were available, and the Berkeley Hills population lies only a short distance from the type locality of the race *californicus*. Hence, previously published descriptions of this race refer essentially to the population I call "Berkeley Hills."

It would have been desirable to choose an *ornatus* population in the uplands north of Suisun Bay. Unfortunately, few specimens are available from this area.

Of those which I have (e.g., four from Davis, Yolo County) all are slightly smaller and paler. Any error in the figures, then, lies in a conservative direction.

The *ornatus* population from the Berkeley Hills is characterized by small, grayish individuals with fragile, low-crowned skulls. Normally, the tips of the hairs are lighter colored than the bases, producing the "pepper-and-salt" effect described by Grinnell (1913, p. 185). Generally, the population is morphologically homogeneous.

*The Grizzly Island population.*

Individuals of *S. sinuosus* from the islands of the Suisun marshes are marked deviates from any other known Californian shrew. Briefly, they may be characterized by saturate, sometimes metallic, black coloration; fragile, relatively narrow and elongate skull; low cranial outline; and long tails. Examination of Figures 2 and 4 and Table I reveal it to be the most homogeneous of the populations under study.

Clearly, topographical as well as ecological insularity contributes to the maintenance of morphological homogeneity in this population. Equally clear is the presence of strong selective forces which yield, perhaps secondarily, the phenotypes described here. The tendency toward darker coloration is found in most tidal marsh isolates in the San Francisco Bay region. This tendency is uniformly expressed without regard to genetic origin of the isolated populations. The tidal sloughs surrounding the Suisun marshes must provide a barrier sufficient to prevent the intrusion of genes from *ornatus* stock. Such intrusion is apparent in the peripheral population next to be described.

*The peripheral population.*

Large areas of tidal marsh vegetation are present on the upland side of the sloughs delimiting the islands of the Sui-

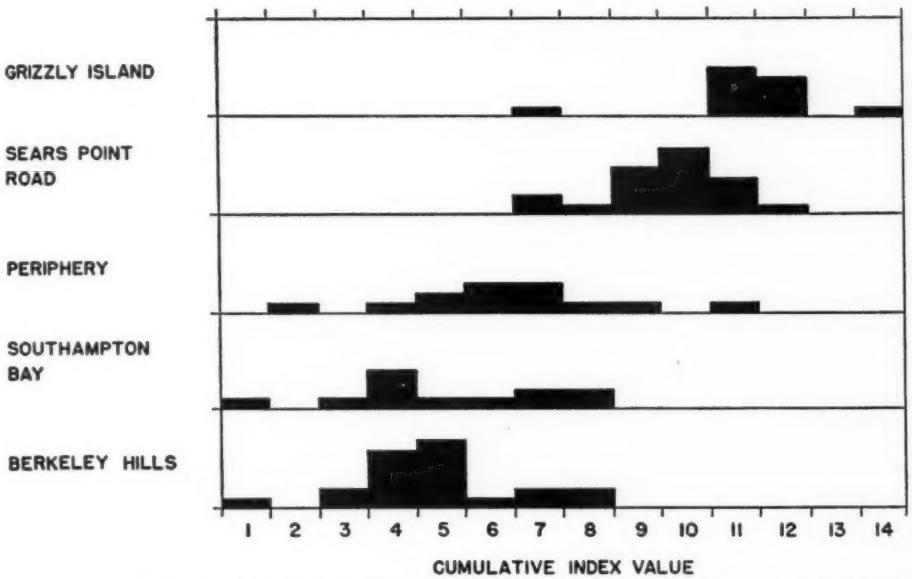


FIG. 4. Frequency histograms of cumulative index values of the same individuals plotted in Figures 2 and 3. The totals of five index values are plotted here. See Table II for value ranges. The vertical distance between abscissae represents ten individuals.

sun marshes. Shrews from this area, when plotted as in Figure 2, show characteristics almost precisely intermediate between those from Grizzly Island and those of upland *ornatus* from the Berkeley Hills. The cumulative index (Fig. 4) shows a lesser shift from the *ornatus* type than does the scatter diagram. Tail length and color are the best expressions of intermediacy. Cranial height falls in the *ornatus* range whereas maxillary tooth row and condylobasal lengths are only slightly greater than *ornatus*.

Intermediacy suggests hybridization. It is difficult to postulate a selective action of different force operating in this population as compared to that on Grizzly Island. The marsh environments are essentially identical. More logically, the characteristics of this population seem derivable from marked introgression of *ornatus* into the *sinuosus* type.

TABLE I—STATISTICAL DATA FOR CHARACTERS AND POPULATIONS TREATED IN THIS STUDY

| | POPULATION | SEX | NUMBER | MINIMUM | MAXIMUM | MEAN | STANDARD DEVIATION | STANDARD ERROR OF THE MEAN | COEFFICIENT OF VARIABILITY |
|---|---|---|---|---|---|---|---|---|---|
| TAIL LENGTH | Berkeley Hills | ♂ | 32 | 29 | 40 | 33.50 | 2.926 | .517 | 8.73 |
| | | ♀ | 29 | 29 | 42 | 34.28 | 2.738 | .508 | 7.79 |
| | Grizzly Island | ♂ | 9 | 37 | 45 | 40.67 | 2.27 | .804 | 5.58 |
| | | ♀ | 10 | 37 | 42 | 39.40 | 2.11 | .703 | 5.35 |
| | G. I. Periphery | ♂ | 7 | 35 | 40 | 37.14 | 1.87 | .763 | 5.03 |
| | | ♀ | 6 | 34 | 38 | 36.33 | — | — | — |
| | Southampton Bay | ♂ | 10 | 32 | 38 | 35.10 | 1.901 | .601 | 5.42 |
| | | ♀ | 3 | 35 | 38 | 36.33 | — | — | — |
| | Sears Point Rd. | ♂ | 27 | 36 | 48 | 41.11 | 3.545 | .682 | 8.62 |
| | | ♀ | 20 | 35 | 46 | 40.60 | 2.885 | .645 | 7.11 |
| | Tolay Creek | ♂ | 11 | 30 | 38 | 36.20 | 1.887 | .597 | 5.21 |
| | | ♀ | 18 | 33 | 41 | 37.24 | 2.209 | .535 | 5.93 |
| | Petaluma Creek | ♂ | 12 | 33 | 39 | 36.83 | 1.972 | .595 | 5.36 |
| | | ♀ | 20 | 28 | 40 | 36.20 | 3.25 | .746 | 8.96 |
| CONDYLOBASAL LENGTH | Berkeley Hills | ♂ | 27 | 15.1 | 16.3 | 15.96 | .355 | .068 | 2.22 |
| | | ♀ | 24 | 15.1 | 16.5 | 15.85 | .377 | .077 | 2.38 |
| | Grizzly Island | ♂ | 9 | 16.3 | 17.2 | 16.74 | .287 | .102 | 1.71 |
| | | ♀ | 5 | 16.0 | 16.8 | 16.44 | — | — | — |
| | G. I. Periphery | ♂ | 7 | 15.6 | 16.7 | 16.21 | .368 | .150 | 2.20 |
| | | ♀ | 6 | 15.4 | 16.4 | 15.96 | — | — | — |
| | Southampton Bay | ♂ | 9 | 15.3 | 16.4 | 15.83 | .406 | .135 | 2.57 |
| | | ♀ | 3 | 15.3 | 16.2 | 15.63 | — | — | — |
| | Sears Point Rd. | ♂ | 18 | 16.1 | 17.0 | 16.63 | .305 | .072 | 1.83 |
| | | ♀ | 14 | 16.2 | 16.9 | 16.56 | .208 | .056 | 1.26 |
| | Tolay Creek | ♂ | 10 | 16.1 | 17.2 | 16.41 | .276 | .092 | 1.67 |
| | | ♀ | 15 | 15.4 | 16.8 | 16.14 | .375 | .100 | 2.32 |
| | Petaluma Creek | ♂ | 12 | 15.6 | 16.3 | 16.01 | .219 | .066 | 1.36 |
| | | ♀ | 24 | 15.1 | 16.7 | 15.93 | .386 | .079 | 2.42 |

TABLE I—Continued

| | POPULATION | SEX | NUMBER | MINIMUM | MAXIMUM | MEAN | STANDARD DEVIATION | STANDARD ERROR OF THE MEAN | COEFFICIENT OF VARIABILITY |
|---|---|---|---|---|---|---|---|---|---|
| CRANIAL HEIGHT | Berkeley Hills | ♂ | 27 | 4.0 | 5.1 | 4.51 | .233 | .045 | 5.17 |
| | | ♀ | 25 | 3.9 | 4.7 | 4.42 | .209 | .042 | 4.73 |
| | Grizzly Island | ♂ | 8 | 4.4 | 4.9 | 4.69 | .160 | .061 | 3.42 |
| | | ♀ | 4 | 4.2 | 4.8 | 4.53 | — | — | — |
| | G. I. Periphery | ♂ | 7 | 4.2 | 4.5 | 4.37 | .137 | .056 | 3.11 |
| | | ♀ | 6 | 4.2 | 4.5 | 4.33 | — | — | — |
| | Southampton Bay | ♂ | 10 | 4.4 | 4.8 | 4.59 | .135 | .043 | 2.94 |
| | | ♀ | 3 | 4.1 | 4.5 | 4.30 | — | — | — |
| | Sears Point Rd. | ♂ | 25 | 4.4 | 5.2 | 4.81 | .207 | .042 | 4.30 |
| | | ♀ | 18 | 4.3 | 5.2 | 4.82 | .271 | .064 | 5.62 |
| | Tolay Creek | ♂ | 10 | 4.5 | 5.1 | 4.83 | .173 | .055 | 3.58 |
| | | ♀ | 15 | 4.4 | 5.1 | 4.70 | .214 | .057 | 4.55 |
| | Petaluma Creek | ♂ | 12 | 4.4 | 4.9 | 4.56 | .118 | .036 | 2.59 |
| | | ♀ | 25 | 4.2 | 4.6 | 4.45 | .122 | .025 | 2.75 |
| MAXILLARY TOOTH ROW | Berkeley Hills | ♂ | 30 | 5.7 | 6.6 | 6.19 | .231 | .042 | 3.73 |
| | | ♀ | 27 | 5.8 | 6.4 | 6.20 | .176 | .034 | 2.84 |
| | Grizzly Island | ♂ | 9 | 6.3 | 6.9 | 6.60 | .224 | .079 | 3.39 |
| | | ♀ | 6 | 6.4 | 6.7 | 6.53 | — | — | — |
| | G. I. Periphery | ♂ | 7 | 6.1 | 6.7 | 6.37 | .238 | .097 | 3.73 |
| | | ♀ | 6 | 6.0 | 6.4 | 6.22 | — | — | — |
| | Southampton Bay | ♂ | 9 | 5.9 | 6.5 | 6.20 | .252 | .084 | 4.07 |
| | | ♀ | 3 | 5.9 | 6.6 | 6.20 | — | — | — |
| | Sears Point Rd. | ♂ | 27 | 6.2 | 6.8 | 6.54 | .185 | .036 | 2.83 |
| | | ♀ | 20 | 6.3 | 6.9 | 6.59 | .169 | .038 | 2.58 |
| | Tolay Creek | ♂ | 11 | 6.2 | 6.6 | 6.37 | .162 | .051 | 2.53 |
| | | ♀ | 18 | 6.1 | 6.7 | 6.46 | .132 | .032 | 2.04 |
| | Petaluma Creek | ♂ | 12 | 6.1 | 6.6 | 6.32 | .128 | .038 | 2.02 |
| | | ♀ | 21 | 5.9 | 6.7 | 6.33 | .212 | .047 | 3.35 |

These data are presented to provide background reference for the graphic material, to show sexual differences, and to illustrate the difficulty in comparing populations with information of this type. Measurements are in millimeters.

*The Southampton Bay population.*

Identification of this population as *S. sinuosus* is largely for convenience. All metric characters fall in the *ornatus* range. A few individuals, however, are much darker than *ornatus*. These examples are shown in Figure 3 but are not identifiable in Figure 4. The cumulative index range parallels that of *ornatus*. There is a difference in pelage appearance which is obscured by the methods of analysis used here. Although the intensity of pigmentation in most individuals is about the same for the two populations, the tips of the hairs are not colored in the same way. Consequently, the Southampton Bay population shows less of the "pepper-and-salt" pattern which appears

TABLE II—MEASUREMENT RANGES OF CUMULATIVE INDEX UNITS

| CHARACTERS | CUMULATIVE INDEX VALUES "0" | "1" | "2" | "3" |
|---|---|---|---|---|
| Cranial Height | 4.1–4.3 | 4.4–4.6 | 4.7–4.9 | 5.0–5.2 |
| Condylobasal Length | 15.1–15.5 | 15.6–16.0 | 16.1–16.5 | 16.6–17.0 |
| Maxillary Tooth Row | 5.8–6.0 | 6.1–6.3 | 6.4–6.6 | 6.7–6.9 |
| Tail Length | 29–33 | 34–38 | 39–43 | 44–48 |
| Color Type *sinuosus* series | 2–4 | 5–7 | 8–10 | 11–13 |
| Color Type Tolay Creek Transect | 1–4 | 5–8 | 9–12 | 13–16 |

Index values are the basis for determining ray lengths in the pictorialized scatter diagrams and for total quantities in the frequency histograms. Measurements are in millimeters.

in *ornatus*. In general, the deviation of characteristics from the *ornatus* type is slight. Slight as it is, this deviation is consistent. (Curiously, slight shifts in characteristics were also noted by Marshall (1948) in song sparrows, *Passerella melodia maxillaris*, from this locality.)

*The Sears Point Road population.*

This population is considered in two contexts: as an example of a distinct *sinuosus* type and, in a later section, as one contributor to a hybrid population.

Shrews from this population are the largest of any under study. Maximum size in all measured characters is the rule for this population. Color is blackish but neither so intense nor so uniform as in the Grizzly Island population. A brownish cast is noticeable in many individuals. This feature considered with high cranium and massiveness of skull gives support to the possibility of noticeable introgression from a *vagrans* type.

Percentage rules have an interesting application in this population. Comparisons of single characters will often show overlap with examples from other populations presented here, but by considering combinations of characters individuals may be identified to population in every case. Although the Sears Point Road population is referable to *sinuosus*, and some overlap is shown in Figures 3 and 4, the separation between it and the Grizzly Island population is total. We need no "70 percent" or "97 from 97 percent" standard to enable identification. Is the Sears Point Road population then to be recognized taxonomically? I think not. The relationship may be more clearly defined by other means. Were it not for prior discovery of the Grizzly Island population, the Sears Point Road animals could have served well as a species type.

*The Tolay Creek Transect*

Three different populations of shrews occupy segments of an environmental continuum on the north shore of San Pablo Bay (Fig. 1). The Sears Point Road population already described is easternmost. The westernmost population occurs at the mouth of Petaluma Creek. Examples from these populations are separable in every case. Between these flanking populations lies Tolay Creek. The shrew population at this locality is extremely variable and includes individuals with combinations of characters unlike those of the adjacent populations.

With the exception of the Sears Point Road population no comparisons are made with populations outside the limits of this transect. Such a procedure was arbitrarily chosen to facilitate analysis of the "hybrid swarm" at Tolay Creek.

Measured characters from these populations are treated in the figures exactly as those from the *sinuosus* series. The color gradient, although the basic scheme is the same, includes individuals from *S. vagrans* and the Tolay Creek population. Individuals were selected from the *vagrans*, *ornatus*, and *sinuosus* populations of the region and arranged in sequence from lightest to darkest. Three color types are young individuals (less than four months of age) from Tolay Creek.

No young animals were included in the specimen samples described here. As might be expected, the gradient was not so easily constructed as one within a species group. Nonetheless, color types array themselves in good relative order.

*The Sears Point Road population.*

Although already described in relation to the *sinuosus* series, this population warrants additional comment regarding its relationship to the other populations in the Tolay Creek Transect.

The scatter diagram (Fig. 6) shows the complete separation of this population from that on Petaluma Creek eight miles distant. The frequency histogram of cumulative index values (Fig. 7) indicates some overlap of population characteristics. Frequency distribution of color types alone (Fig. 5) also shows a slight overlap. It is appropriate to point out here the error of interpreting relationships from any single means of analysis. There is, in fact, no difficulty in separating individuals from these populations. They are obviously different forms.

*The Petaluma Creek population.*

Individuals from this locality are characterized by grayish-brown pelage, moderate tail length, short rostra, relative massiveness of the interorbital area, and low cranial outline. I refer to this population as *S. vagrans,* as indeed I believe it to be. However, many of its characteristics are *ornatus*-like. Small size, low-crowned cranium, and general coloration support such relationship. In support of assignment to *S. vagrans* are such characteristics as short rostrum, wide interorbital region, and relative massiveness of this region. The "good characters" used to separate *S. ornatus* and *S. vagrans* do not hold when applied to this population. I refer specifically to the height of the metacone of the third upper premolar and the position of the foramen magnum. Variation in these characters within the population is too great to lend comfort to the systematist attempting their use. Certainly, this population requires further comparison before assignment of taxonomic status. In any event, my interest in this paper centers in the contribution which this population makes to that at Tolay Creek.

*The Tolay Creek population.*

A glance at the frequency distribution of color types (Fig. 5) reveals the essential characteristic of the Tolay Creek

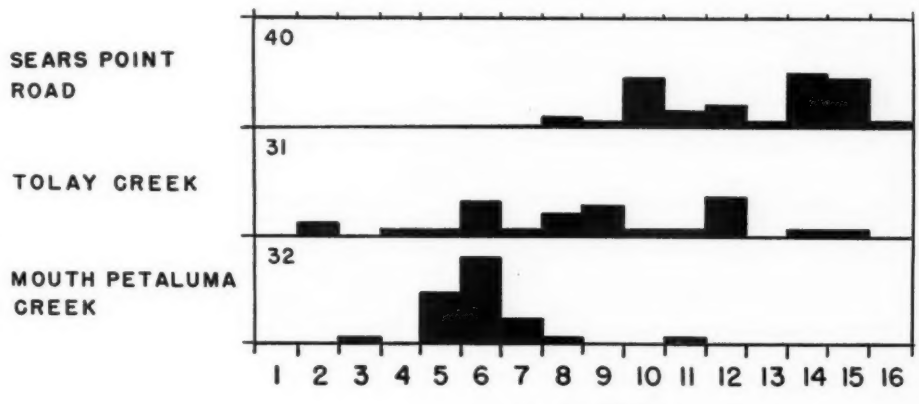


FIG. 5. Frequency histograms of color types from three populations in the Tolay Creek Transect. Numbers of individuals plotted are indicated at the upper left in each histogram. The vertical distance between abscissae represents twenty individuals. The gradient of color types cannot be compared directly with that in the *sinuosus* series.

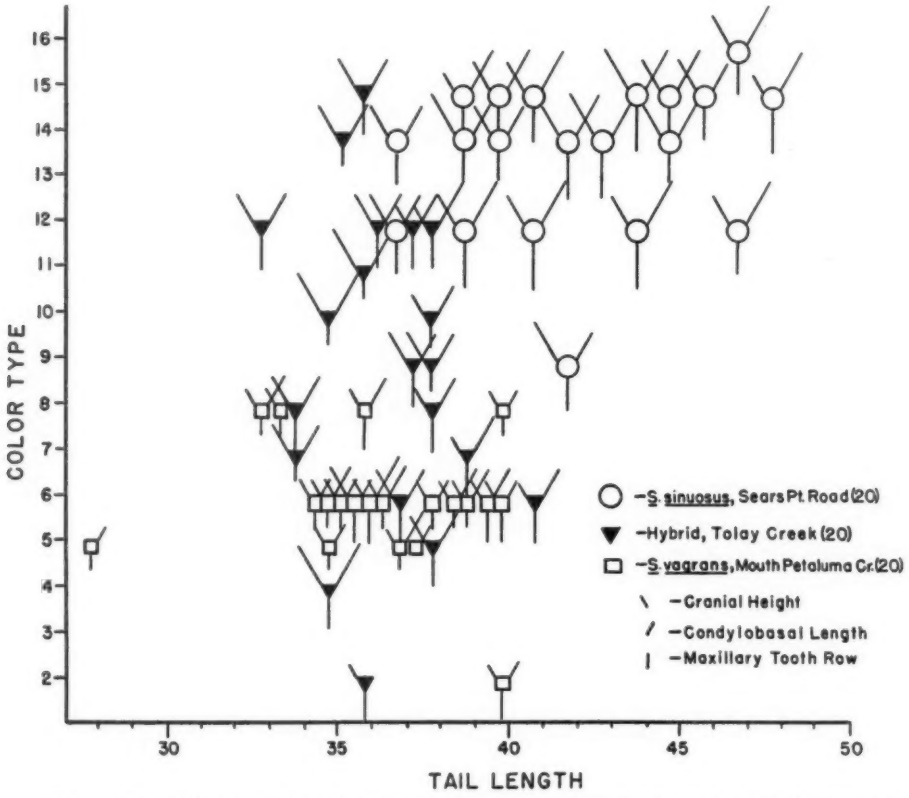


FIG. 6. Pictorialized scatter diagram of three populations in the Tolay Creek Transect. See Figure 2 and Table II for description of method. Ten adult males and ten adult females from each population are plotted.

population. The expression of single characters at Tolay Creek approaches, and in some characters exceeds, the ranges of the flanking populations combined. Close inspection of Figure 6 discloses an intermediate position of cranial measurements in most individuals. Many individuals, however, show combinations of traits which are not found in the adjacent population (e.g., a dark individual with maximum cranial height and short tooth row; or the palest individual in the Tolay sample with maximal expression of skull length but minimal tooth row length and low cranial height).

It is unnecessary to characterize this population morphologically; the figures do this ably. The figures and Table I support the hypothesis of extensive hybridization. With the exception of tail length the majority of individuals fall into an intermediate range. Even color, which is so variably expressed, chiefly occupies a central range on the gradient (most individuals are included between color types 6 and 12).

## *Discussion*

### *Relationships of populations.*

Measurable differences between local populations have been described in many groups of animals. Such differences have

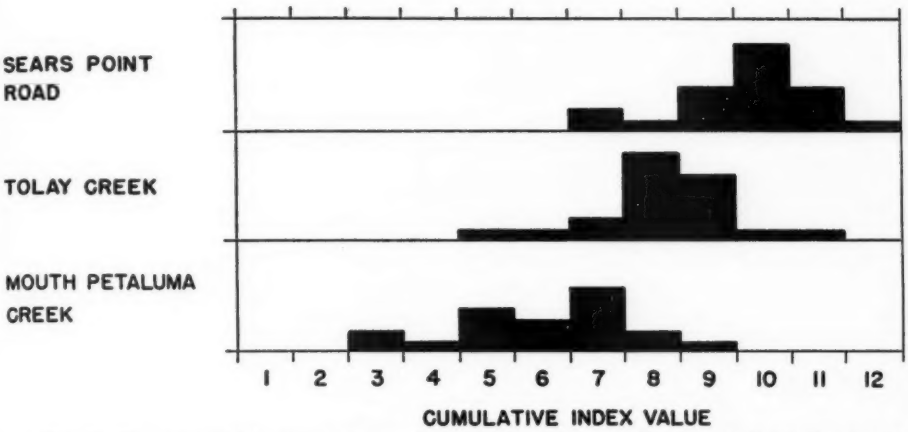


FIG. 7. Frequency histograms of cumulative index values of the same individuals plotted in Figure 6. The totals of five index values are plotted here. See Table II for value ranges. The vertical distance between abscissae represents ten individuals.

been recognized in small mammals, although precise studies on this type of differentiation are few. Local population deviates occur more commonly in mammals whose ecological tolerances are narrow. Large populations of shrews can be maintained only where extensive low-lying plant cover and an abundant invertebrate food supply exist. The tidal marsh environment satisfies these requirements best of those habitats available in the San Francisco Bay region.

The populations of *S. sinuosus* have some unique features. The most obvious of these concerns the distribution of the species. I have described all known populations of a species having a very restricted distribution. Yet within this restricted area, further delimitation is easily possible. Every isolate (a *deme* in the literal sense) may be consistently characterized.

Isolation, without question, is the first condition allowing local differentiation. The marsh environments are strikingly simple and similar. Adaptive requirements must be closely equivalent in all such marshes irrespective of the degree of topographic isolation. Selection would operate in parallel fashion on all marsh isolates. Differences between populations are derived from the differing genetic constitutions of the original invading stocks. After establishment of populations, varying degrees of contact with adjacent populations would contribute further to these differences. Opportunities for contact may be sporadic or continual. The population at Tolay Creek probably results from recent contact between types which have been previously separated. The marginal population, "Periphery," shows the effect of continual contact where selective action and continuing gene intrusion are in approximate balance.

The strong expression of increased size and darker coloration which characterizes some of the *sinuosus* populations suggests a selective force of great magnitude. But as at Southampton Bay, for example, small populations do not seem to be as subject to this selective force. Whether this is a function of small population size or of greater opportunity for contact with adjacent upland types is an open question. The upland habitat about Southampton Bay is as forbidding as that about the Suisun marshes. Quite obviously, assuming the opportunity for contacts to be the

same at the two localities, continual genic intrusion from *ornatus* stock would be better reflected in the Southampton Bay population than in those of the Suisun marshes.

Two populations—"Periphery" and Tolay Creek—are clearly of hybrid origin. Clearly, too, the populations have not been produced in the same manner. The population at the edge of the Suisun marshes may be looked upon as a "primary intergrade" (Mayr, 1942) or a product of "allopatric introgression" (Anderson, 1953). Hybridity of this type is expected in the zones of contact of allopatric races. Qualifications must be made in this instance, however. If primary intergradation is indicated here, it takes an odd form. Taxonomically at least, we are dealing with two species. This point will be discussed later. More importantly, the transition from *ornatus* to *sinuosus* type is abrupt. Although character gradients exist, these may not be termed clinal in the usual meaning of the word. Character differences are extreme within a short distance, perhaps three or four miles. Greatest significance may be ascribed to the ecological discontinuity which occurs between upland and marsh localities. Grizzly Island not only supports a high shrew population of homogeneous nature but is isolated from other shrews. The peripheral population although inhabiting essentially the same marsh is not isolated topographically from upland shrews. The flow of genes is toward the more favorable marsh environment. Shrews from marshes apparently are subject to a different set of selective influences from those to which shrews from the upland are subject. Differential selective action operating at the junction of two sharply dissimilar habitats apparently succeeds in restricting population variability.

The Tolay Creek population, on the other hand, is highly variable. The flanking parental populations are well established and presumably well adapted to the tidal marsh environment. No sharp ecological discontinuity exists in the Tolay Creek Transect. It may be that survival of hybrid recombinants is enabled in part by parallel adaptive proclivities in the parental populations. Contact between the populations at Sears Point Road and Petaluma Creek is probably relatively recent. It is unlikely that differentiation occurred in the marshes of this Transect as presently constituted. The great variability of the Tolay Creek population may be a manifestation of this recency of contact. I might comment at this point that the condition of a newly formed, variable population adjoined in a continuous environment by two different types offers an unusual opportunity for future study. Sampling the Tolay population at periodic intervals may disclose shifts in gene frequencies more narrowly delimiting the contributions of the individual introgressants.

*Nomenclatorial considerations.*

The local populations of *S. sinuosus* do not warrant taxonomic status as long as they can be conveniently grouped under a recognized name. Their characteristics and relationships are better shown by the methods used in this paper than by hierarchical designations. The only question which might be raised concerns the species rank granted *sinuosus*. I suggest that this status remain unchanged. The suggestion is based on two practical considerations. First, reduction of *sinuosus* to a trinomial would obscure the fact that this assemblage of populations is a natural unit. I say this recognizing fully that some of these local deviates may be separated with greater reliability than can recognized races in many mammals. Secondly, irrespective of our conceptual doubts about the practice, degree of morphological divergence remains the primary index to the proper placement of populations in the systematic order. On this premise specific rank is justified. Until recently the only specimens of *sinuosus* available came from Grizzly Island. Consider the views of two able zoologists who have examined these speci-

mens critically. Grinnell (1913, p. 180) in his description of this form refers to it as ". . . the remarkable new species *Sorex sinuosus*." The latest monographer of the genus (Jackson, 1928, p. 171) recognized *sinuosus* as ". . . easily distinguishable from any other member of the *ornatus* group." Most mammalogists would quickly second these statements.

Discussion of the nomenclatorial status appropriate for the restricted populations described herein has particular meaning in the context of recent commentaries in this journal (Wilson and Brown, 1953; Edwards, 1954; Mayr, 1954). In general, I feel that little is accomplished by lending formal rank to restricted populations where these types may be defined by other means. They are better treated by geographic or pictorial designations. In this view I accord with Wilson and Brown. Notwithstanding, I am by no means prepared to discard trinomial designations hastily. Inadequate as they are generally recognized to be, they remain the best expression of infraspecific relationship within poorly worked groups. Paucity of specimens and difficulties of analysis will plague us continually. I regard the trinomial not as an immutable biological unit meriting perpetual priority but as the expression of an historical stage in the progressive refinement of our knowledge of the speciation process. Imposition of a formal terminology not following priority rules (the natios, forms, morphs, etc. of Edwards, 1954) contributes greatly to an already overburdened terminology and does little to enhance understanding. The material under study and the ingenuity of the examiner should dictate the best method of analysis of infraspecific variation (*cf.* Sibley, 1954, p. 110). Rigid dependence on formal standards is stultifying, not edifying.

## *Summary*

Four populations of *Sorex sinuosus* are described and characterized by means of pictorialized scatter diagrams and cumulative indices. A population of *S. ornatus* from which *sinuosus* is presumably derived is treated in like manner for comparison. Each of the populations may be separated from the other by appropriate combinations of characters. Two intermediate populations reflect continuing contact with upland *ornatus*. The most marked deviates (Grizzly Island and Sears Point Road) exhibit black coloration, long tails, and large size. Isolation and large population size are considered important requirements for the maintenance of population characteristics.

A hybrid population exists at Tolay Creek where a distinct type of *S. sinuosus* comes into contact with a markedly different animal of the *S. vagrans* group. All three types live in tidal marsh which is essentially continuous. The distance between parental populations is about eight miles.

Current systematic treatment is adequate to express general relationships in these shrews. Nomenclatorial adjustments are not necessary. Infraspecific populations of the type described here are best defined by geographic or pictorial means. This is particularly true of restricted populations. Use of the trinomial name is warranted in poorly known groups where more accurate means of defining population relationships are not available. Its use is not required when adequate study materials and more refined methods of analysis permit a better concept of relationship. Rigid adherence to nomenclatorial standards—with or without priority rules—is undesirable in the study of infraspecific variation.

Specimen material used in this study was obtained from the following sources: Museum of Vertebrate Zoology, University of California, Berkeley; Department of Zoology, University of California, Davis; Los Angeles County Museum; California Academy of Sciences, San Francisco; and D. R. Dickey Collections, University of California, Los Angeles. I wish to thank the custodians of these collec-

tions for their courtesy in making specimens available. S. B. Benson and O. P. Pearson were particularly helpful in the earlier phases of this study. G. Ledyard Stebbins provided me with valuable comments on analytical methods and interpretations.

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## Random Fixation in Fleas

(*Concluded from page 47*)

population was reduced to an extremely low level and temporarily isolated. Then, it may have been possible for a different form to appear within a very small area, while other fleas close by maintained their original appearance.

This conclusion has been drawn by conjecture and without conclusive evidence for the theory, but it may be surmised that explanations such as individuals from other areas somehow being transported through a narrow corridor, or establishment of a new subspecies in a small area where there are no visible barriers, as in northwestern New Mexico, do not satisfactorily account for the presence of this flea. Anomalous, aberrant, or dimorphic specimens are common among some fleas but they occur singly and have not been reported in series taken twice from any particular locality. Random fixation, then, seems most logically to apply to this problem.

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# Sympatry, Allopatry, and the Subspecies in Birds

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IN HIS recent controversial paper on infraspecific categories, Edwards (1954) included a short section on "Cross-breeding between members of different subspecies." The present paper will discuss some aspects of this and certain related phenomena, using birds as examples. The term "subspecies" as used here is as accepted by Mayr (1954) and many others, not the restricted term proposed by Edwards.

Edwards sought to limit the term "subspecies" to distinctly allopatric populations, removing from this category those populations which intergrade where their geographic ranges overlap. This, he believed, would eliminate the necessity of establishing fixed mathematical standards of separability for nomenclatural recognition (the "75 percent rule" and similar propositions). In birds, however, and I suspect in other groups as well, strict allopatry is not a guarantee of complete or even partial morphological divergence within a species. Some bird species include two widely allopatric populations which appear to the taxonomist to be identical. An example is the white-faced whistling duck, *Dendrocygna viduata*, which has populations in both South America and Africa. Gene exchange between these two populations is unlikely, to say the least, yet the birds from the opposite sides of the Atlantic appear to be identical. In other cases these widely allopatric populations have diverged slightly, but not to an extent worthy of nomenclatural recognition by any modern standard; an example is the Holarctic pintail, *Anas acuta* (Parkes, 1953). At the opposite extreme are allopatric populations which exhibit a complete divergence in one or more characters. Many of these were originally described as separate species, and some older taxonomists continue to uphold such a viewpoint. Selecting an example among the ducks again, we have the well-marked forms of the green-winged teal, *Anas crecca;* the Palearctic *A. c. crecca*, and the Nearctic *A. c. carolinense*. It must be remembered that examples might be found of almost every intermediate stage of differentiation, in completely allopatric populations. In a population which is almost wholly separable from an allopatric conspecific population, individuals may appear which resemble those of the latter in their taxonomic characters. If such individuals are at all numerous, we find ourselves invoking some mathematical subspecies criterion, *even among allopatric populations.*

The mobility of many birds makes it necessary to conjecture as to the origin of the occasional individual of population "B" which more closely matches population "A" in its characters. Do such individuals represent an expression of the gene pool of the population from which they were collected, or are they actually wandering individuals of the population whose taxonomic characters they display? Rand (1948) treated in some detail the problems involved in identifying individual specimens taken away from the breeding area; it boils down to a matter of mathematical odds as to whether the moot specimen which looks like the majority of population "A" did, in fact, derive from that population, or whether it is actually one of an "A"-like minority of population "B."

In connection with the special case of a wandering individual actually remain-

ing to breed among a population of a different subspecies, Rand stated: "It seems that the wandering individual, itself, would . . . change its status." While I agree with Rand that the *progeny* of such a bird would, in many cases, "probably be absorbed in the population in which it bred and would become part of it, perhaps adding to its variability," I cannot subscribe to a change of status for the parent. This bird is genetically a member of the population (subspecies) inhabiting the region where it was hatched, regardless of what sort of mate it may choose.

We can say little about the ultimate genetic effect on a population of the assimilation of an occasional genotype from another subspecies, simply because we do not yet know enough about the genetics of wild birds. The number of genes and modifiers involved in the production of a given phenotypic character and the relative dominance of various alleles are questions at which we can but guess. We do have evidence that fairly frequent "straggling" contact between spatially isolated populations may retard or prevent differentiation of those populations, as postulated by Edwards (1954, p. 12). This is best illustrated among insular birds; the populations of outlying islands are often more sharply differentiated than are those of the same species from islands close enough together to permit a significant amount of straggling. Amadon (1950, pp. 165, 235) has shown this in the case of the Hawaiian honeycreeper *Loxops virens*. In this species the populations of nearby Maui, Lanai, and Molokai are inseparable; those of Hawaii and Oahu, respectively, are quite distinctively colored; and that of outlying Kauai is characterized by a bill "much stouter than that of the others."

Members of the same species have been traditionally supposed to be completely interfertile. This assumption is a basic part of Edwards' restricted definition of the geographic subspecies (1954, p. 12): ". . . whose respective members would cross-breed rather freely and normally if the populations were sympatric under natural conditions." More and more evidence is accumulating, however, to show that certain physiological adaptations, often not reflected in physical appearance, may hinder viability of offspring when individuals from widely separated portions of the range of the species are brought together and crossed; especially notable is the work of Moore on frogs. If a similar phenomenon obtains in birds, it is possible that the introduction into a population of the genotype of another subspecies may have little or no ultimate effect because of reduced viability of the hybrid offspring. Again, there is presumably an adaptive significance in, or correlated with, most observable geographical differences in morphology and physiology, with selection acting to stabilize a more or less constant gene frequency in a population. The hybrids resulting from the breeding of our theoretical wandering individual may have an embryological viability as high as that of the parents; however, there may be selection acting against them as juvenile or adult birds, since their phenotypes will differ from the presumably optimum one which has been stabilized in the population.

An illustrative case in point is that of the bob-white, *Colinus virginianus*. This small game bird is now all but extinct in most of New York and New England. At least part of this extirpation was, of course, due to hunting pressure, although the bob-white survives in the southern states where it is the principal game bird. There is a widely held opinion that the introduction by man of bob-whites from the southern portions of the range of the species has so diluted the native northern stock as to render it unfitted for the rigorous winters of New England and upstate New York. This factor was mentioned by earlier authors such as Eaton (1910, p. 364) and Phillips (1915), and by more recent writers such as Todd (1940, pp. 172–175) and Cruickshank (1942, p. 152).

Aldrich (1946) commented extensively on the effects on native populations of bob-whites and other game species of introduction of different subspecies. His thesis seems to be that the introduced stock is "swamped out" by the better-adapted native stock, and that after a few years no trace can be found of the birds exhibiting the external characters of the introduced subspecies. His examples, however, were taken from areas where a sufficient native population remained to make such a "swamping" possible (Georgia, Pennsylvania, Maryland). A far different situation prevailed in such areas as New England, on the periphery of the species' range, where severe winters such as that of 1904–1905 would decimate the native population, and southern birds would be brought in to *replace* these. The imports might thus, at the time of liberation, actually outnumber the hardy survivors of the native bob-whites in the area, even though a good many of these southern birds probably died before they had a chance to breed.

Aldrich emphasized external morphological characters in his attempt to detect influences of hybridization on native populations. The all-important physiological attributes of the birds which will determine whether they can survive a rigorous climate are invisible. As Aldrich himself stated (p. 92), ". . . birds of two regions may appear similar enough to be considered the same race, yet may have small physiological differences (not reflected in outward appearance) in response to slightly different environmental conditions which would render them unsuited to survival in another region." The same thing may well be true of hybrid versus native bob-whites in the northern states.

Birds, for many reasons, are far from being ideal subjects for laboratory experiments in genetics. It is conceivable, however, that a sufficiently endowed institution might set up a long-term program whereby studies could be made on the interbreeding of conspecific birds from various parts of the range of the species. Some attempts have been made along these lines on a small scale, as in the genus *Junco* (Miller, 1941, pp. 372–373).

In many widely distributed bird species of the Northern Hemisphere, the northernmost populations are the most migratory, while some southern populations may be virtually sedentary. Since the nesting season of northern birds must, for obvious reasons, commence later than that of southern birds, it may frequently happen that migrants of a northern population are passing through an area when the resident birds have already started to nest. In some cases these migrants may readily be separated from the local birds by external characters, and have been validly described as subspecies on the basis of comparison of breeding birds of both populations. In other cases the northern and southern populations may be indistinguishable when breeding examples are compared. In some species there are seasonal changes of plumage or of soft-part colors which are correlated with the stages of the reproductive cycle. In these cases, although specimens at the same stage of the cycle may be indistinguishable, the resident birds may be distinguished from northern migrants present in the same area by their advanced reproductive condition. It was this phenomenon which led Bullough (1942, p. 241) to separate the resident starling population of the British Isles as a "physiological subspecies," *Sturnus vulgaris britannicus*. I believe it to be a mistake to separate as a formally named subspecies a population of birds differing from the rest of its species only in the timing of its reproductive cycle. Such populations could almost certainly be detected within the range of many widespread species.

To return to the possibility of sporadic hybridization of subspecies, actual examples might be chosen from among a number of avian species. Taverner (1942, p. 235) presented a particularly lucid discussion of this phenomenon and its impli-

cations in the great horned owl, *Bubo virginianus,* a species much addicted to wandering. The race of red-winged blackbird native to the northern prairies (*Agelaius phoeniceus arctolegus*) occurs casually on migration in central and western New York, an area well within the breeding range of the subspecies *A. p. phoeniceus.* A female specimen in the Cornell University collection, taken at Danby, New York, on May 8, 1949, is a typical *arctolegus.* Its ova were enlarged. It is possible that this was a late migrant of *arctolegus* which would have continued on its way northwest. On the other hand, it was taken at a locality where *phoeniceus* breeds abundantly, and in view of its advanced reproductive condition it may well have remained to nest. A similar case involving two western subspecies of *Agelaius phoeniceus* was described by van Rossem (1926, p. 222).

It is obvious that such subspecific interbreeding cannot be proved without actual collecting of mixed mated pairs. It is, however, possible to demonstrate inferentially that such interbreeding may well have taken place, principally by the identification of intermediate individuals. It must be understood that I am not discussing the hybridization of adjacent populations along a common boundary or zone of intergradation. The problem here involves the sporadic breeding of individuals or small numbers of birds among a population well removed from that of their origin.

A pertinent species to the present discussion is the green-winged teal, *Anas crecca,* mentioned earlier in this paper. The European subspecies, *A. c. crecca,* is now a rare but fairly regular visitor to Long Island, New York, and it has been recorded at points along the Atlantic coast from Labrador to South Carolina. Here it comes into contact with the American subspecies, *A. c. carolinense.* Males of the two subspecies are quite distinctively colored, but females are almost indistinguishable, even in the hand. Cruickshank (1936) reported that males of both races may be seen courting the same female on Long Island, displaying identical courtship behavior. That an ocasional *crecca* will accompany *carolinense* north to its breeding grounds is suggested by the descriptions of intermediate-plumaged individuals published by Cruickshank (1936) and Poole (1940, p. 578).

The small northwestern subspecies of red crossbill, *Loxia curvirostra sitkensis,* has invaded the northeastern United States in great numbers in certain winters, notably those of 1887–1888, 1940–1941, and 1950–1951. I have examined typical specimens of *sitkensis* taken in the state of New York during each of these major irruptive flights, and collected several myself during the last one. We have, of course, no way of knowing whether these flocks of birds returned to their normal northwestern breeding range in the spring. That all individuals did *not* do so is suggested by three *sitkensis* collected at Ithaca, New York, as late as May 16, 17, and 20, 1941. I have seen no specimens from the 1950–1951 invasion taken after March 25, but there were several later sight records of red crossbills in areas of central New York where *sitkensis* had been collected during the winter.

Another subspecies of red crossbill, *L. c. minor,* breeds more or less regularly in the coniferous forests of northern New York, New England, and northeastern Canada. It differs from *sitkensis* in having a larger body size and a proportionately larger and differently shaped bill. I have examined (through the courtesy of William C. Dilger) three adult male red crossbills taken at Ithaca, New York, on April 29, 1953. These three specimens match large *sitkensis* in weight and wing-length. Their bills, however, appear to be intermediate in size and shape between the two races *sitkensis* and *minor.* It is possible that these adult birds represent the offspring of members of the great *sitkensis* flight of 1950–1951 which did not return to the northwest but remained within the breeding range of *minor* and

mated with individuals of the latter subspecies.

It is evident that the museum curator, in his routine identification of specimens, is often obliged to acknowledge a number of alternative biological possibilities, and to accept what seems to be the most probable interpretation for each particular case. Neither the taxonomic relationships nor the geographic distribution of birds is as simple to describe as was once believed. Bird-banding has shown, for instance, that small numbers of certain species, especially among the ducks, gulls, shearwaters, and other water birds, may regularly cross the Atlantic Ocean, once believed to be almost the ultimate in geographic barriers. As we accumulate additional knowledge through collecting, banding, and field observation, we find it necessary to alter from time to time, sometimes quite radically, our concepts of the geographic distribution, characters, and relationships of many species and subspecies. I believe that this can be done within the framework of the present system of trinomial nomenclature, by admittedly maintaining the subspecific category as flexible to reflect its flexibility in nature.

Most attempts at further and more rigid definition of infraspecific forms appear to me to be attempts to create categories where no categories exist in nature. The choice seems to be between a broad subspecific category within which we may acknowledge various evolutionary stages, and a myriad of terms to account for all such possible stages even though these blend into one another completely. I believe the former to be the more practical course. I also agree with Mayr (1954, p. 88) that the several recent proposals to eliminate the subspecies category altogether cannot be considered improvements. Mayr's short paper summarizes a common-sense approach to difficult taxonomic situations, and should be thoroughly absorbed by those whose impatience with current systematic terminology and practices has led them to propose radical innovations.

*Summary*

1. It is not practical to restrict the term "subspecies" to strictly allopatric conspecific populations in order to avoid the use of a mathematical standard of separability, since all degrees of differentiation may be found among allopatric populations.

2. Occasional specimens of birds taken within the breeding range of one subspecies but resembling another may be either stragglers of the latter or variants of the former.

3. Such stragglers may remain to interbreed with the population whose range they have invaded. Such cases can seldom be demonstrated without actual capture of mixed mated pairs, but can be deduced from examination of intermediate individuals.

4. The ultimate genetic effect of such introductions of foreign genotypes is little known. Different physiological or morphological adaptations of the parental types may result in either reduced viability of the offspring or selection against them.

5. Physiological differences of a temporal nature (i.e., breeding cycle) can probably be demonstrated within any widely distributed species, and should not be used as a sole subspecific criterion.

6. Although much criticism has been leveled against the trinomial system of nomenclature, it appears to be the best working compromise if used flexibly, with due acknowledgement of the several stages of evolution now embraced in the subspecies concept.

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# An Invitation to Systematic Zoologists

The Pacific Oceanic Fishery Investigations[1] with headquarters in Honolulu is engaged in a program of exploration, investigation, and development of the high seas fishery resources of the central Pacific. Of fundamental importance to our research program is the relative productivity or amount of basic fish food in different ocean areas. Since the inauguration of field work in 1949, our attempts to measure quantitatively the abundance of organisms at the various eutrophic levels have yielded extensive collections of zooplankton, fish, and miscellaneous invertebrates.

We have employed a variety of sampling methods and types of gear; plankton nets, pelagic trawls, light traps, dip netting around a light, hand lining, and poison (rotenone) have all been used. The stomachs of tunas, marlins, lancet fish, etc., have been a rich source of organisms not collected by the usual methods. While we have sampled a number of environments—lagoons, coastal reefs, and shelf areas adjoining the oceanic islands—our work in the upper layers of the open ocean from the surface to a depth of several hundred meters has been most intensive and extensive. We have not explored the deeps nor dredged the bottom.

In those collections that lend themselves to quantitative analysis, the constituents have been sorted into major taxonomic groups, counted or the number estimated, and their displacement volumes determined. The counts and volume data have been used in comparing the standing crop of potential fish food in different ocean areas with particular hydrographic features of the environment and with the abundance of tunas as determined from our experimental fishing.

Although not primarily concerned with systematic zoology, we have made a diligent effort to identify the organisms as precisely as practical. Those forms that were prominent in our collections and considered important items of fish food were usually identified to species, frequently with the help of specialists at the University of Hawaii and the Bernice P. Bishop Museum. However, for many groups the taxonomy is not well organized and most of our material is only classified to genus or family, in the case of the fishes, and to family or order in the invertebrates.

Certain families of the fishes, special

*(Concluded on p. 42)*

[1] U. S. Department of the Interior, Fish and Wildlife Service.

# "The Language of Taxonomy"

R. E. BLACKWELDER

*THE LANGUAGE OF TAXONOMY. By John R. Gregg. Columbia University Press, New York, 1954.* 71 pp. $2.50. (Bound.)

THE encouragement of scholarship and the conditions conducive to the birth of new truth were the theme of Columbia University's bicentennial celebration last year. Among the samples of the University's scholarship that are being published to signalize this event, there is one of great potential interest to systematists.

*The Language of Taxonomy* by John R. Gregg, Associate Professor of Zoology at Columbia, is a very small book. It is not one, however, which will be read and understood in a short time by anyone except a logician. It solves none of the problems of taxonomy; it will not answer the questions currently arising between systematists. Nevertheless, this book may well prove to be the clue to the solution of some of these important problems.

Taxonomy is the study of kinds of organisms. This book is an attempt to develop a language for use in taxonomy. It is therefore not a book on taxonomy but on metataxonomy—the study of taxonomic statements. Taxonomy and metataxonomy differ in having different subject matters, in having different vocabularies, and in being unequally developed. This book is an attempt to develop one aspect of metataxonomy by illustrating the utility of set-theory concepts in the study of taxonomic classification.

In order to present examples of the application of the theory of sets, Gregg finds it necessary to outline the principles of this subject, which is one of the symbolic methods of formal logic. The resulting semimathematical expressions can be made explicit and definable, thus circumventing the unsuitable prescientific idioms borrowed from everyday language which have heretofore led taxonomists into endless semantic difficulties.

Set-theory is one of the methods of logic which can emphasize for the taxonomist the distinctions between kinds, classes of kinds, and categories of classes. Confusion between the latter two, or failure to distinguish them clearly, seems to be at the root of much of taxonomy's difficulties over the reality of species and the philosophic nature of the higher categories. Dr. Gregg has not set out to solve these difficulties in this book, but rather to present the basis for a language which will be suitable for conveying such a solution.

Dr. Gregg has pointed out to the reviewer an error that might not be obvious even upon close study. In the footnote on page 47 a definition of "taxonomic classificatory system" is proposed that is intended as an improvement upon the definition given in the main body of the text. Owing to printer's omissions, the new definition is not adequate as it stands, but matters will be set right by replacing each of the two occurrences of "$z$" in the fourth line from the bottom of the page with "$*z$." (The sign "$*z$," designating the ancestral of the relation $z$, is defined on page 24.) Thus restored, the new definition states in effect that any relation ordering a set of taxonomic groups may be regarded as a taxonomic system provided that the following conditions are satisfied: (1) there is one all-inclusive group in the set; (2) any two groups in the set stand in the relation only if one immediately includes the other; and (3) given any two groups in the set, either they have no members in common or else one bears the ancestral of the relation to the other.

The reviewer believes that the diffi-

culties described in the concluding paragraph of the book, resulting from apparent category overlapping and its complication of the relations between the levels of a taxonomic system, are not real. The trouble arises from the fact that Simpson, in the segment of classification used by Gregg as example (page 35), used certain short-cuts which leaves room for misinterpretation of his ideas of category relationship. If the difficulty proves not to be real, some slight changes in statements and inferences will need to be made on pages 35–40 and on pages 61–68. Apparently these will not affect the validity of the general presentation of set-theory usefulness in metataxonomy.

*The Language of Taxonomy* is recommended to all those who are interested in the semantics of taxonomy or the philosophy of classification. The inclusion of explanations of elementary set-theory principles and concepts makes it somewhat independent of other works, but the reader who is unfamiliar with symbolic logic must be willing to learn, from the early chapters, part of its distinctive language and procedures.

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## An Invitation to Systematic Zoologists

*(Concluded from p. 40)*

groups of the invertebrates, and aliquots of zooplankton collections have already been made available to students and other research workers at the University of Hawaii and the Bernice P. Bishop Museum, and to specialists at several institutions on the mainland of the United States. The bulk of our collections, however, have not been thoroughly worked over. We now have on hand specimens representing about 95 fish families and practically all of the major invertebrate groups. We also have extensive zooplankton collections, unsorted except for removal of extra large organisms and tuna eggs and larvae. It is our desire that this material receive the fullest possible use, and we believe that thorough taxonomic treatment will uncover many forms new to science, make a significant contribution to our knowledge of Pacific fauna, and provide information needed in our research program.

Therefore, we invite the participation of taxonomic specialists. We will pack and ship any portion of our collections to a qualified investigator who can give the material his prompt attention and who will undertake to provide us with certain information we need. He may use the material to further his own studies in any way he chooses and may publish his findings as he pleases. In many instances the published paper, in the form of reprints, will furnish the information we need. We may ask, in addition, interim lists of species, annotated as to collection station and numbers of individuals.

While in the hands of the investigator the specimens will be in a loan status. The collections are the property of the United States Government and their eventual disposition is governed by law. When the investigator has completed his study, the final distribution of duplicate series or sets of specimens will be decided jointly by the United States National Museum and the United States Fish and Wildlife Service, although consideration will be given to any recommendations the investigator may choose to make.

The first set of identified specimens and also the holotypes of all new species will be transferred by the United States Fish and Wildlife Service to the United States National Museum. In many instances, the Fish and Wildlife Service will also request the return of a set of identified specimens for reference purposes. An equitable distribution will be made of all remaining duplicate series or sets of specimens.

We invite correspondence indicating the field of interest and requesting material.

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# Points of View

## Are Coelenterates Degenerate or Primitive?

"A Reconstruction of Animal Classification" appeared in SYSTEMATIC ZOOLOGY for December 1953, representing the conclusions of Jovan Hadži. At the 1954 meetings of the A.A.A.S. it became evident that these conclusions were receiving serious attention. Some of them have been accepted for at least a decade. In the December 1954 issue of SYSTEMATIC ZOOLOGY G. S. Carter offers some excellent amendations to Hadži's scheme. Some additional questions, however, still plague me, and perhaps plague some others.

That Coelenterates are degenerate rather than primitive is Hadži's strong contention, and this is extensively based on the notion that radial symmetry cannot be primitive, that it must be ecologically and secondarily determined.

The Porifera are brushed aside with the casual remark that "genetically the sponges have nothing in common with Coelenterata." It so happens that my research specialty has long been the Porifera, thus this is interesting to me. It does indeed appear certain that sponges evolved from a different set of Protozoa from those which evolved into Coelenterata. Yet evolution must have been somewhat the same process in both cases. The point is that the next step above the unicellular level certainly can have radiate symmetry, because that is exactly the case for Porifera. The sponges retain radiate symmetry throughout their entire life unless the environment spoils it. Furthermore, their sessile existence, if it does anything, always spoils their radial symmetry, never increases it! This should be recalled in connection with further remarks to be made below. We can learn from study of sponges. Radiate symmetry is primitive in them; why may it not be primitive in the other animals that are least different from them?

Hadži reiterates that becoming sessile causes a population to assume radial symmetry. For example, he says "radial symmetry has developed in many lines as a consequence of transition from free life to a sessile existence"; also, "Sessile and, therefore, radially symmetric Cnidaria must be derived from bilaterally symmetric animals which led a free life and possessed free locomotion." This deserves to be closely examined.

Hadži accurately states and properly regrets that *Hydra* has been commonly regarded as at the stem of the coelenterate phylum. Its availability for inland universities has given it undue attention. My study of sponges has focussed my attention on the sea, and it is there that most coelenterates live. It seems clear that *Hydra* is a peculiar offshoot, just as the few freshwater sponges are highly specialized but not the best representatives of their phylum. The typical coelenterate is the jellyfish. *Hydra* almost certainly is degenerate, as claimed. But it is not a degenerate planarian, rather it is a degenerate descendant of medusae. It is not, however, newly radiate because sessile; the more primitive jellyfish is emphatically free-living, with vigorous locomotion, and radiate.

It is here maintained that assumption of sedentary life has little or no tendency to produce the radial body plan. Radiate symmetry arises from primitive genetic tendencies in that direction.

Study of the tunicates is important to an evaluation of the results of becoming sessile. Many species of this subphylum

are much more sedentary than such Cnidaria as sea anemones. Yet study of the adult sea squirts reveals that they are emphatically bilateral in symmetry.

One could not ask for a better example of the assumption of sessile life than that which is afforded by the Cirripedia. Far back in geologic time the barnacles became utterly sedentary, yet their continued evolution, with profound adaptation to this existence, has left them pronouncedly bilateral.

The phylum Mollusca is replete with sedentary forms, going back to Paleozoic times. Clams, mussels, and especially oysters, illustrate extreme adaptation to sessile life, but with not a trace of progress toward or tendency to, radiate symmetry.

The phylum Echinodermata does exhibit many cases of radiate adults with bilateral larvae. This should be carefully studied in comparison with the coelenterate radiate adults with bilateral(?) planulae. The significant fact is that the adults in question are not sessile, and whatever causes the radiate symmetry to appear, it is not loss of motility. Anyone who has tried to capture brittle stars in tidepools knows how agile are these radially symmetrical animals. Asteroids and holothuroids are not quite so active as the ophiuroids, but are far indeed from being sessile; even sea urchins travel.

Recapitulation in embryonic life is an interesting subject. The human embryo, with tail, mesonephros, and gill-like structures, clearly albeit sketchily recapitulates the same vertebrate evolution that is illustrated in the fossil record. Higher animals in general, as embryos, have a diploblastic stage. This struck me, as a student, as strongly suggestive of the basic body plan of the jellyfish. When it was first noticed in the nineteenth century it forcibly so impressed the pioneering explorers of embryology. It is still worth consideration. Unfortunately Haekel took his usual sort of part in this matter. He paid much attention to the sponges, and left maddening confusion wherever he intruded there. He made beautiful illustrations that are, however, so conventionalized that they are either actually false, or at best misleading. His attention to embryology has similarly left much need for correction. The British have a maxim: "Don't throw out the baby with the bath water." We no longer wash Junior in a pan, but the figure of speech remains graphic. There has been a tendency in correcting Haeckel's extravagance to discard also the germ of truth that was present.

The diploblastic embryo significantly resembles Coelenterata, but the existence of the planula larva has encouraged zoologists to disregard this significance. Many, including the Yugoslavian expert, assume that the planula is a recapitulation of a planarian-like ancestor to the Cnidaria. Did evolution proceed via a never-diploblastic route to Platyhelminthes, and then recede to diploblastic Coelenterata?

The planula does bear superficial resemblance to a planarian, but so does a worm resemble a snake. Hadži specifically and dogmatically states that the Coelenterata ancestors had, and that the Coelenterata have lost, such structures as sense organs, ganglia, complex muscles, and nephridial organs. There are compound ascidians that certainly have had and certainly have lost such structures, but these latter show in the larvae. I cannot find even any vestiges of such organs in the planula, and must regard Hadži's notion as lacking evidence.

Has the planula bilateral symmetry? By some definitions, yes, but does it have significantly bilateral symmetry? It has no paired or left and right organs. The earlier morula and blastula have radial symmetry. By delamination the latter becomes full of endoderm cells. It may settle to the bottom and become motile as a result of its cilia. It now proves to be plastic and it may well be that its flattening is merely the result of this plasticity. The somewhat older embryo is clearly radiate. Rather than saying that it went through three stages, radiate to bilateral to radiate, it would be simpler, and I be-

lieve more accurate, to classify it entirely as radial.

It is written that in the Trachymedusae and Narcomedusae the zygote develops directly into the free-swimming, radiate adult with no planula stage. It is worth considering that this may be the primitive or ancestral condition.

Neoteny is a hazardous basis for evolutionary theories, and should be relied upon only when the evidence is quite clear. For example, did we not have the fossil record, it would be quite plausible to argue that fish are paedogenetic mammals.

Analysis of what Hadži says in various places reveals his claims that Protozoa evolved into highly organized Turbellaria, that some of these then degenerated into sessile polyps, then that some of these evolved into free-swimming medusae. It has been widely doubted that evolution ever reverses itself that way. One would like to have strong evidence before removing the doubt.

The fact that the great Yugoslavian zoologist has spent forty years in intensive study of modern coelenterates may actually have been a slight handicap. This is due to the fact, which he wisely acknowledges, that the modern forms are not the ancestral ones. They have had hundreds of millions of years in which to change from their own ancestral types, for example, in the development of their elaborate cnidoblasts.

The evidence from embryology still deserves consideration, in spite of the disservice rendered to it by Haeckel. I believe that we should be very cautious in forming theories that contradict this evidence. We may well believe that the ancestors of all the higher groups (including our own), shortly after rising above the protozoan level, arrived at one that may be called the coelenterate level. They were not modern coelenterates, emphatically not hydras, but were simple, diploblastic and radial. Were such ancestors still available in some museum, the systematist could appropriately put them in the same case or phylum with the coelenterates.

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## Random Fixation as an Explanation for a Unique Population of Fleas

Now that the theory of random fixation (Wright, 1940 *a*, *b*) has gained wide acceptance, its use in explaining various problems arising during systematic studies makes the theory of highest practical value. This paper is an attempt to evaluate in the light of this theory the status of a group of fleas of peculiar morphological characteristics and of limited distribution within the normal range of recognized subspecies of fleas.

Although random fixation of genes is not a common phenomenon, one situation favoring this action is the great fluctuations in population size to which fleas are subjected. Elton (1930, pp. 77–83) has illustrated how the nonadaptive "blue" mutant became established in populations of arctic foxes during extreme reduction of the population by famine. While it is not known whether the characteristics of the flea being discussed in this paper are nonadaptive, it is here supposed that random fixation may serve to explain an unusual deviation in a pattern of distribution. There have been several contributions from the better-known studies of mammal, bird, and plant populations as

evidence in favor of random fixation. Systematic studies in entomology are now entering and contributing to new fields of study as some of the many orders of insects are becoming better known.

Through the western half of the United States certain ground-squirrel fleas show typical formation and distribution of subspecies. These fleas are now referred to as separate species and a few as subspecies of *Thrassis bacchi gladiolis* (Jordan 1925). It is hereby proposed to group all these related fleas as subspecies of *Thrassis bacchi* (Rothschild 1905). There is conclusive evidence of clines existing throughout most of the ranges of these subspecies.

The map of western United States (Fig. 1) shows the ranges of these subspecies, together with drawings of the ninth sternum of five of the subspecies. The lobe of the ninth sternum, as shown in each drawing, is one characteristic among several that may be used to separate each subspecies. Each drawing represents a subspecies found in its respective shaded area, which is indicated by an arrow, and demonstrates the morphological relationship in conjunction with the geographical relationship.

*Thrassis bacchi bacchi* (Rothschild 1905) occurs in the Dakotas, Montana, Wyoming, and part of Colorado; *T. b. caducus* (Jordan 1930) occurs principally in Utah; and *T. b. gladiolis* (Jordan 1925) in southwestern United States, west of the Colorado River. The two laterally placed bristles on the ninth sternum are found gradually to be nearer the apical bristles when the specimens are examined consecutively in order of geographical occurrence, starting from San Diego and proceeding to the northeast, until in *T. b. bacchi* of the Dakotas, all three bristles are grouped together.

Other distinguishing morphological characters show the same patterns of distribution, as well as the same clinal

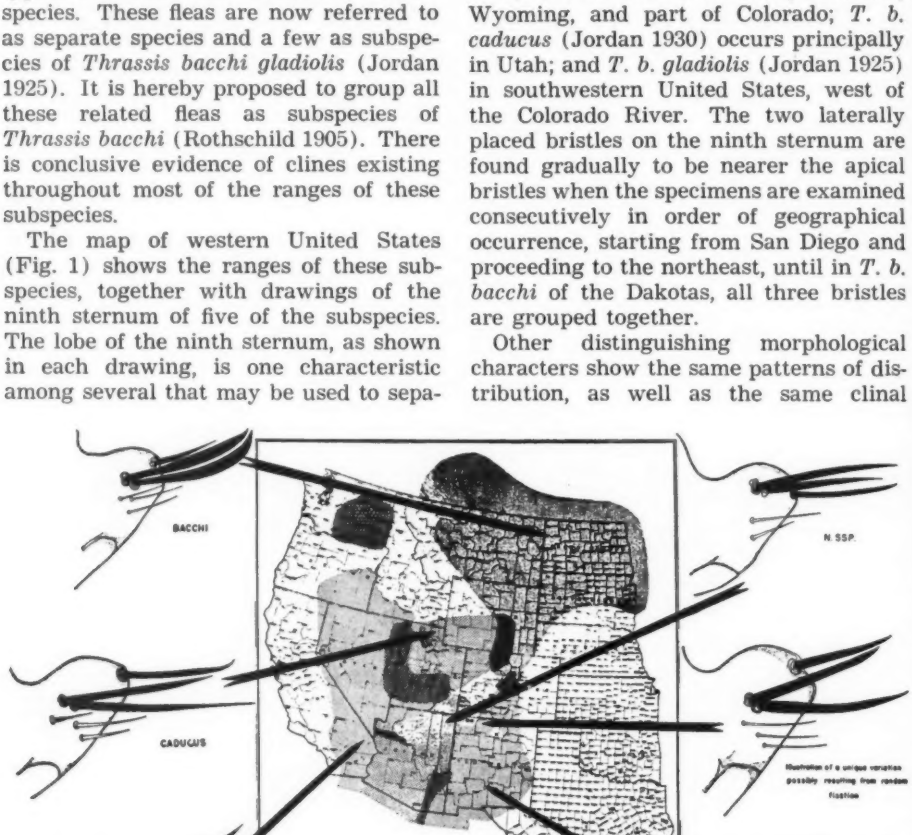


FIG. 1. Ranges of the subspecies of *Thrassis bacchi* (Rothschild 1905) with drawings of the ninth male sternum of each subspecies. The dots represent the two collecting sites of the unique population in San Juan Co., New Mexico. The cross indicates the locality of the possible intergrade with *Thrassis bacchi pansus* at Alcade, New Mexico.

tendencies. For example, the eighth tergum of *T. b. pansus* (Jordan 1925) of New Mexico bears but three or four bristles, while that of *T. b. setosis* Prince 1944, distributed through southern Arizona, bears up to eight or nine. When the specimens are plotted geographically, there is a gradual to sudden increase in number as one proceeds from east to west, indicating a step cline. *T. b. new ssp.* (a subspecies yet to be described) occurs to the north of *pansus* and *setosis*, showing evidence of intergradation with *setosis*. A seventh subspecies, *T. b. johnsoni* (Hubbard 1949), found in Washington is ecologically isolated on the vole, *Lagurus curtatus*, and is without clines. It is morphologically allied to *T. b. gladiolis* of California, Nevada, and Oregon.

Twice, an odd flea of this *T. bacchi* complex was taken in northwestern New Mexico in San Juan County (Fig. 1). This flea occurs virtually within the range of distribution of *T. b. new ssp.* and *T. b. pansus*. Adequate sampling has substantiated the ranges of fleas to the west and south of the occurrence of this unusual flea, but to the north and east there are few collection data. There is, however, evidence of intergradation between *T. b. bacchi* and *T. b. pansus* in Park County, Colorado, thus giving further evidence in favor of clinal tendencies and subspeciation among the typical fleas in this area. The two collections of this flea, represented by the two dots, were made within 24 miles of one another; one collection consisted of a male and a female, and the other was a series containing thirteen males and two females. When the close proximity of its more typical neighboring relatives is considered, it may be assumed that this variation is probably confined to a very small area. However, this flea demonstrates considerable morphological differences from the other typical neighboring individuals, represented by hundreds of specimens in the material studied. (Ninety-two specimens of the new subspecies is the smallest number available for study.)

The ninth sternum (Fig. 1) is somewhat like *caducus*, as found far to the north in Utah, but otherwise differs in several respects from other fleas of this complex. Furthermore, the variation probably is not a pure strain. Variation existing among two specimens of the thirteen males consists of the lateral bristles of the ninth sternum being placed closer to the apex on one side only, causing bilateral asymmetry.

One significant fact is that the presence of this flea appears to cause a break in the sequence or pattern of clinal distribution that seems to be uniform throughout most of the range of this *T. bacchi* complex. Two main groups appear to have been formed (possibly from *T. b. bacchi* of the Dakotas): one group west of the Colorado River, and the other group along the eastern margin of the Rockies to the southwest desert region east of the Colorado. To the west and south the modified bristles of sternum IX of the male are more widely separated from the apical bristle, whereas in those to the east and south all bristles remain close to the apex; other features display increasing clinal variation from *T. b. bacchi*. An abrupt geographical relationship of morphological differences in this complex is evident from collections along the Colorado River between Arizona and California where there is an obvious barrier and the end products of evolutionary migration appear evident. The one exception to the trends along the Rockies and the Colorado River is the unique population in this discussion.

A single male of *T. b. pansus*, collected near Alcade, New Mexico (indicated by a cross on map), shows clinal tendencies to the peculiar variation in San Juan County and not to the typical new subspecies found to the north and to the west. This single specimen may be or may not be of significance.

Random fixation appears to be the most plausible explanation. The evidence above suggests that at some time in the past the

*(Concluded on p. 34)*

# People and Projects

The first volume of a projected series of twenty, entitled *The Insects of Micronesia*, has recently appeared. The Bernice P. Bishop Museum, Honolulu, is sponsoring this series, and J. Linsley Gressitt of that institution has undertaken the editorial supervision of this project in which over 115 specialists will cooperate. The Arachnida and Crustacea will be included in addition to the Insecta. Subsequent volumes will contain a bibliography of Micronesian entomology and the systematic reports of the collaborators. The reports will be published in the order received, although the volume numbers will be assigned in accordance with the systematic position of the contents. A general summary of the zoogeography of the area will complete the series.

The introductory volume by Dr. Gressitt delineates the geography, geological history, and biotic environment of Micronesia. This provides a background which will be invaluable to the specialists preparing the systematic reports as well as to the interested reader.

A small crustacean, the characteristics of which are widely divergent from those of any known group, has been assigned to a new subclass, Cephalocarida, by its discoverer, H. L. Sanders. Sanders has reported upon the external anatomy of his find in *Proc. Nat. Acad. Sci.*, Vol. 41, No. 1, pp. 61–66. Specimens were taken at various times in muddy bottom beneath shallow water (9–20 meters) off the north shore of Long Island Sound. The new species, *Hutchinsoniella macracantha*, bears a superficial resemblance to a harpacticoid copepod, but on close examination is seen to be unlike copepod, branchiopod, or malacostracan, although exhibiting some similarity to each. The Cephalocarida are defined as "Crustacea with a large head posteriorly covering the first thoracic segment, with significantly more [19] postcephalic segments than in the Malacostraca (which have fourteen or fifteen), with biramous appendages but no abdominal pleopods." Sanders concludes, on the basis of a careful examination of the external anatomy, especially the appendages, that this new form "may be looked upon as an extremely primitive crustacean at about the same level of complexity as the Branchiopoda but probably related to the ancestral stock that gave rise to Copepoda, Branchiura, and possibly the Malacostraca."

*Erratum.* In the program for the 1954 annual meeting of the Society of Systematic Zoology, which occupied this department of the December 1954 issue (p. 186), the institutional affiliation of Edward L. Kessel is incorrectly stated. Dr. Kessel is chairman of the Department of Biology at the University of San Francisco.

The University of Maryland announces the offerings of the Institute of Acarology for the Summer Session, 1955, from 27 June to 16 July. Since the inception of this program at Duke University in 1951, it has provided a unique opportunity for entomologists, parasitologists, and zoologists to learn about mites and ticks. In line with the recent important discoveries of the role of the Acarina in the fields of public health and agriculture, the program now has been expanded to be of greater service by increasing the facilities and the staff and by the participation of investigators from nearby institutions. The staff this year consists of Edward W. Baker, U. S. Department of Agriculture; Joseph H. Camin, Chicago Academy of Sciences; and George Anastos and G. W. Wharton, of the University of Maryland. Further information can be obtained from G. Anastos, Department of Zoology, University of Maryland, College Park, Maryland.

**SYSTEMATIC ZOOLOGY** is published quarterly by the Society of Systematic Zoology. Its purpose is threefold: To publish, and therefore to encourage the preparation of, contributions on basic aspects of all fields of systematics, principles and problems; to provide a suitable forum for discussion of the problems of the systematist and his methods; and to report as news the other activities of the Society of Systematic Zoology.

Contributions of the following types are solicited: Papers on principles and the applications of principles of wide implication and general interest in any phase of systematics, such as comparative anatomy, zoogeography, paleontology, taxonomy, classification, evolution, or genetics; discussions of methods, specific problems, and activities of systematists; discussions of new books and monographs; and news of systematists, organizations interested in systematics, research and teaching programs, expeditions, collections, meetings, and anything else of interest to systematists.

Consult recent issues for the style to be followed in the preparation of manuscripts. Contributors are encouraged to submit line drawings and diagrams to illustrate their articles. Half-tones may be accepted where necessary to the article.